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Bulletin of the British Museum (Natural History)

Zoology series Vol 35 1979

British Museum (Natural History)
London 1979

Dates of publication of the parts

No 1	26 April 1979
No 2	26 April 1979
No 3	26 April 1979
No 4	31 May 1979
No 5	28 June 1979

ISSN 0007–1498

Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

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E. G. Easton

Zoology series Vol 35 No 1 26 April 1979

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Parts are published at irregular intervals as they become ready. Volumes will contain about three hundred pages, and will not necessarily be completed within one calendar year.

Subscription orders and enquiries about back issues should be sent to: Publications Sales, British Museum (Natural History), Cromwell Road, London SW7 5BD, England.

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

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ISSN 0007-1498

Zoology series
Vol 35 No 1 pp 1–126

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 26 April 1979

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A revision of the 'acaecate' earthworms of the *Pheretima* group (Megascolecidae: Oligochaeta): *Archipheretima*, *Metapheretima*, *Planapheretima*, *Pleionogaster* and *Polypheretima*

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Synopsis

Following the studies on the *Pheretima* group of Asio-Australasian earthworms by Sims & Easton (1972), those genera lacking intestinal caeca, *Archipheretima*, *Metapheretima* (inc. *Ephemitra*), *Planapheretima*, *Pleionogaster* and *Polypheretima*, are examined by taximetric procedures. One hundred and fourteen nominal species and subspecies are reviewed; 75 species are regarded as valid and a further 25 are described as new. Keys, descriptions and distributions are provided to the genera and species. The morphological development and structural specializations of the male pores are detailed and their taxonomic importance is discussed. The nephridial systems of several species are described and doubt is expressed about the validity of attributing classificatory significance to these characters. The distribution of the *Pheretima* group of genera is established in the context of plate tectonics and the restrictions are correlated with present day climatic factors.

Introduction

Sims & Easton (1972) employed numerical techniques to detect phenetic assemblages within the genus *Pheretima* auct. which at that time included 746 nominal species. From their studies on a sample of 114 species, they concluded that eight genera should be recognized. Four, *Archipheretima* Michaelsen, 1928, *Ephemitra* Sims & Easton, 1972, *Metapheretima* Michaelsen, 1928 and *Planapheretima* Michaelsen, 1934, contained species lacking intestinal caeca and the remaining four, *Amynthas* Kinberg, 1867, *Metaphire* Sims & Easton, 1972, *Pheretima* Kinberg, 1867 (*sensu* Sims & Easton, 1972) and *Pithemera* Sims & Easton, 1972, accommodated species with caeca on the intestine. The authors assigned the nominal species previously included in *Pheretima*

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auct. to species-groups within these genera although they did not attempt to describe or taxonomically revise the individual species.

This report is a continuation of those taximetric studies and contains the results of critical appraisals of all the taxa included in the 'acaecate' genera (*Archipheretima*, *Ephemitra*, *Metapheretima* and *Planapheretima*) also the closely allied monotypic genus *Pleionogaster* Michaelsen, 1892. After full investigation, the genus *Metapheretima* is now redefined to include *Ephemitra* and some of its species are assigned to *Polypheretima* Michaelsen, 1934, previously a synonym. Numerical procedures similar to those employed by Sims & Easton (1972) were adopted to test the phenetic validities of the genera and to detect infra-generic groups. Descriptions, synonomies and distributions are given of 100 valid species which are recognized among the five genera investigated. The higher systematics and zoogeography of the acaecate genera are briefly discussed.

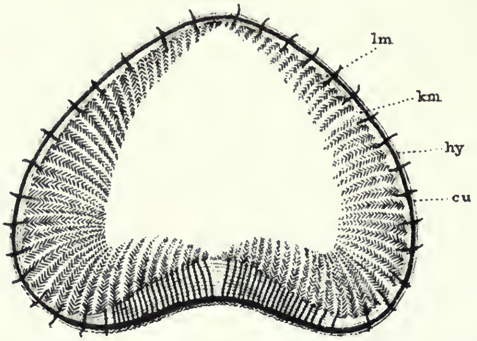

Fig. 1 *Planapheretima hasselti*, transverse section of body. *lm*, longitudinal muscle; *km*, circular muscle; *hy*, epidermis; *cu*, cuticle. (From Horst, 1883.)

Morphology

An account of the morphological features observed to vary among the species of the *Pheretima* group of genera and found to be useful for delineating taxa was provided by Sims & Easton (1972). Since then the taxonomic significance of variations in setal number, segment size and number of spermathecae has been demonstrated by Easton (1976). During the course of the present investigation it became apparent that further morphological specializations can usefully be employed for generic and specific recognition. The following require comment.

1 Body shape

The body shape of most species is approximately circular in cross-section although it may be flattened or concave ventrally in the region of the genital field. The spasmodic contraction of the *archiform muscles* (Oishi, 1930) in the more anterior segments during preservation may in particular give the body a flattened appearance. The majority of species included in *Planapheretima* are arboricolous, these too have depressed bodies but with the longitudinal muscles grouped in paired lateral blocks (Fig. 1). (Associated with this condition are cryptic coloration, crowded ventral setae and often a glandular ventral surface forming a 'creeping sole'.)

It is assumed that the diameter : length proportion is constant for individuals of all species of the *Pheretima* group killed by a standard method (excluding regenerating specimens) as established for *Amynthas hupiensis* by Grant (1955).

2 Setae

Examination of long series of individuals show that, in the *Polypheretima elongata* species-complex, the number of setae on segment *vii* is positively correlated with the volume of that segment and that two groups of taxa may be recognized with different setal densities (Easton, 1976). In *Metapheretima sentanensis* and *M. triciae* the setal densities are considerably higher and they form a third group (Fig. 2). Unfortunately the majority of other species discussed in this report are known only from one or few individuals. Nevertheless, it is possible to assign these taxa to one or other of the three groups recognized on the basis of data derived from the examination of a single individual. The number of setae increase posteriorly usually to about segment *xxx* and then decrease in number to the posterior end of the body (Beddard, 1895 : 291; Hatai, 1924; Sivickis, 1930). These variations are not included among the taxonomic criteria employed in the present revision.

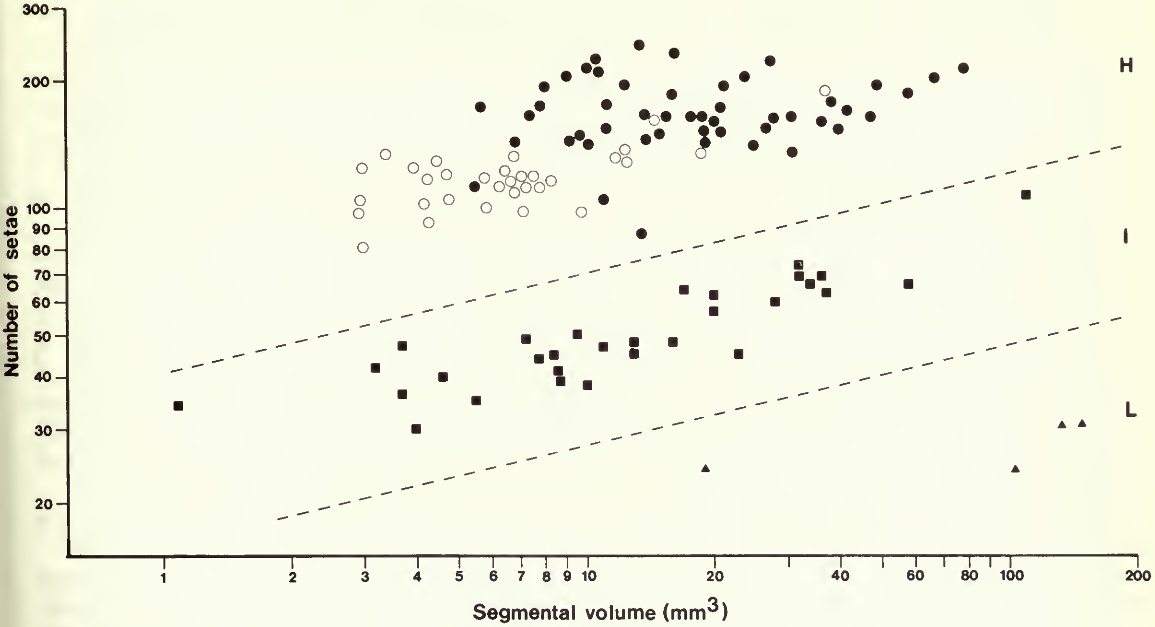

Fig. 2 Correlation between the number of setae and segmental volume of segment *vii* (scales logarithmic). Setal densities: *L*, low (*Polypheretima kinabaluensis*); *I*, intermediate (*P. elongata, everetti, phacellotheca* and *stelleri*); *H*, high (closed circles – *Metapheretima sentanensis*, open circles – *M. triciae*).

The setae are usually situated in a single ring around the equator of each segment, but in a few species of *Planapheretima* and *Metapheretima* some may be displaced to form two or three rings. In most species the setae are regularly distributed around each segment, being rarely crowded ventrally or dorsally. However, in the majority of species of the genus *Planapheretima* the setae are densely crowded ventrally (see *Body shape*).

The ventral and dorsal gaps in the setal ring (*aa* and *zz*) are often larger than the adjacent gaps (*ab* and *yz*) but seldom exceed twice the size of the adjacent gaps; exceptionally in *Archipheretima* they are much larger and in *A. ophiodies* the dorsal gaps are equal to one quarter of the body circumference. The conventional setal nomenclature has been followed throughout (Stephenson, 1930).

Penial setae occur rarely in the *Pheretima* group of genera and are unknown among the acaecate species.

3 Dorsal pores

The location of the first dorsal pore is fairly constant in most species, usually occurring in the region of 11/12 but it may be in any furrow between 5/6 and 13/14, even 19/20 in the case of *Polypheretima coplandi*.

4 Clitellum

The clitellum is usually restricted to three segments (*xiv–xvi*) but it may begin on *xii* or *xiii* and extend posteriorly to *xvii* or *xviii*. The clitellum is annular on segments *xiv–xvii* but may be incomplete ventrally on *xii, xiii* or *xviii*. All of the species of *Polypheretima* as well as the majority of *Metapheretima* have clitella restricted to three segments. All of the species of *Archipheretima* and *Pleionogaster* have extended clitella as do most of the species of *Planapheretima*. Occasionally clitella are found to be poorly developed in fully grown individuals. This condition is believed to be characteristic of a postsexual phase (Gates, 1972*a* : 318).

5 Male pores

The species investigated may be divided into two groups on the basis of the structure of the male pores. In the first, each male pore is situated in the centre of a circular or oval papilla, the porophore, which is often pigmented; crescentic genital markings are never associated with these pores (while the spermathecal pores are always small). In the second group the male pores do not discharge through porophores and crescentic markings are often present (here the spermathecal pores may be small or large).

In both groups the male pores may have accessory structures which show a wide range of intra- and inter-specific variation. Among these diversifications it is possible to recognize a morphological series of increasing complexity in each group ranging from a simple superficial pore to a condition in which the pore discharges into a copulatory pouch. In a separate study of the ontogenesis of species possessing the more complex pore structures, it was found that during development each individual passes through successive growth phases which represent the condition of adults of less highly specialized species. The structure and development of the copulatory pouches in the two groups differ yet the developmental processes are sufficiently similar for the two to be regarded as an example of parallel development.

(*a*) *Male pores on porophores.* The total range of variation in the structure can be traced during growth in *Polypheretima elongata* and, in the case of the more complex structure, *P. koyana.*

In the immature condition (Fig. 3a–b) the circular porophore of *elongata* is faintly demarcated with a poorly discernible crescentic ridge enclosing the porophore. With increased maturity both the porophore and the ridge become more distinct (Fig. 3c). During the next phase the porophore begins to invaginate along its lateral margin while its median edge often becomes raised above the surface of the body (Fig. 3d). At its maximum development in *elongata*, the porophore is almost completely enclosed leaving only a characteristic crescentic aperture to the copulatory pouch visible on the body surface (Fig. 3e). In this species the copulatory pouch is restricted to the body wall and does not invade the coelom; the porophore occupies the medial wall of the copulatory pouch.

Juvenile individuals of *Polypheretima koyana* have copulatory pouches indistinguishable from those described above in mature adults of *elongata* (Fig. 3e). With increasing maturity the aperture to the pouch of *koyana* becomes a longitudinal slit and develops tumid lips while the porophore occupies the floor of the pouch (Fig. 3f). Insufficient material of this species is available to allow intermediate stages between figures 3e and 3f to be recognized.

Male pores are on porophores in all species of *Polypheretima* as well as some species of *Archipheretima* and *Planapheretima*. The porophores may be within copulatory pouches in species of *Polypheretima*. However, it is possible that when more mature individuals become available for study some of the species which are noted as having simple male pores will be found to have more complex structures.

Chen (1946) described the porophores of *Planapheretima continens* as occasionally bearing a penis-like structure (Fig. 3g), this species has not been examined. However, during the examination of an individual of *elongata*, a similar structure was observed which proved to be an artifact caused by an incomplete removal of the cuticle.

(*b*) *Male pores lacking porophores.* The stages in development of the male pore present in the species lacking porophores are represented in a series of individuals of *Metapheretima kilii* and, in the case of the most complex condition, *M. oinakensis.*

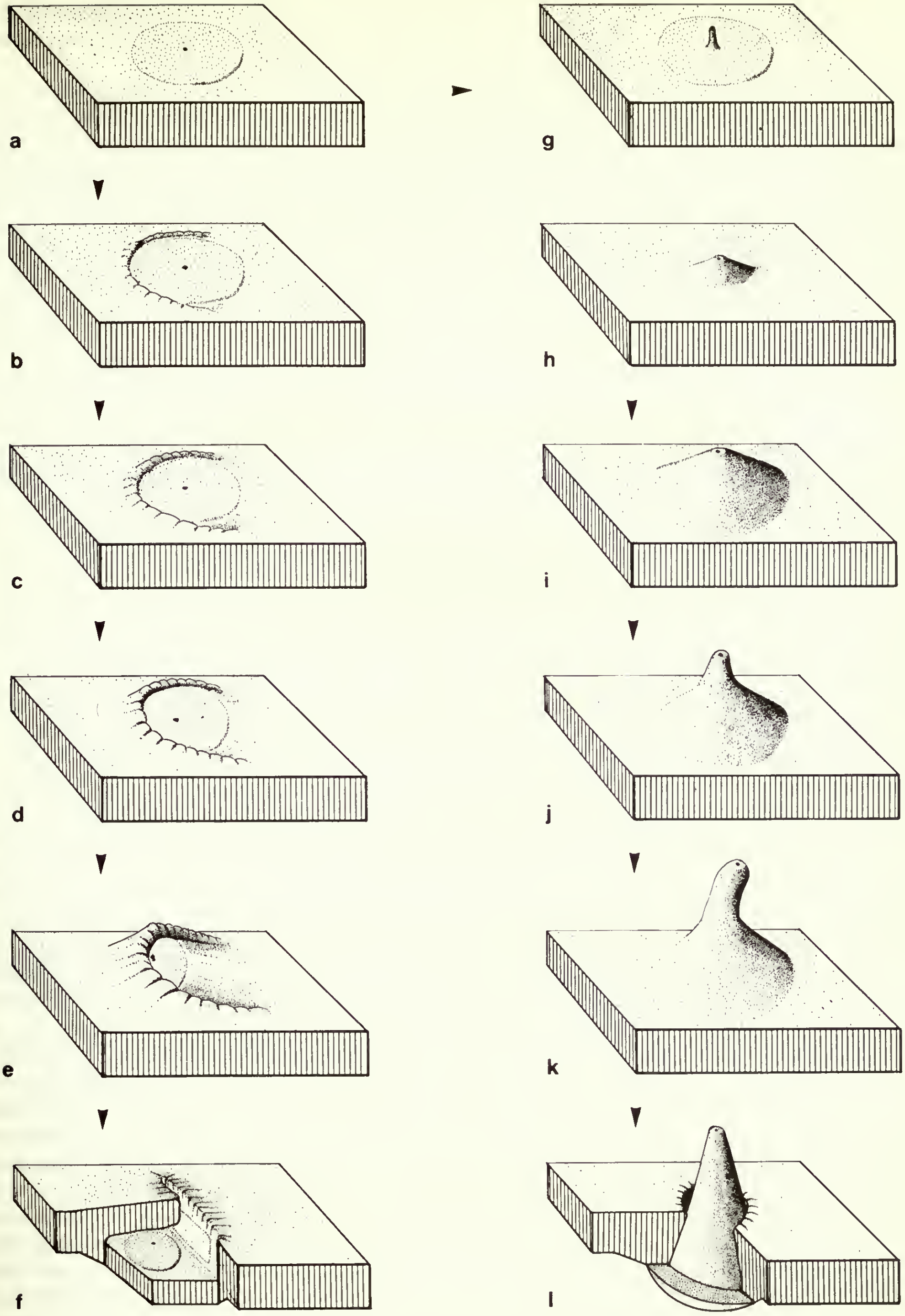

Fig. 3 Development of male pores. (a–f) *Polypheretima*; (g) *Planapheretima continens*; (h–l) *Metapheretima*.

In an immature individual of *kilii* the male pore is at the centre of a low conical body (Fig. 3h). With increasing maturity the conical body increases in size and elevation (Fig. 3i), and the upper portion finally develops into a slim, penis-like structure (Figs 3j–k).

In *oinakensis* the male pore is terminal on a slim penis similar to that found in *kilii* (Fig. 3k), but it is incorporated within a copulatory pouch (Fig. 3l). The intermediate stages by which this form of copulatory pouch develops are unknown, but in view of its different structure they are unlikely to be similar to those found in *elongata*. Development possibly involves the invagination of the body wall around the whole periphery of the basal end of the penis.

Male pores lack porophores in all species of *Metapheretima* and *Pleionogaster* and some species of *Archipheretima* and *Planapheretima*. The male pores may be in copulatory pouches in species of *Metapheretima*. Several species (*Metapheretima deirdrae*, *jocchana* and *sembaluensis*, *Pleionogaster horsti*. *Planapheretima maculata*) have male pores considerably larger than those usually encountered.

In two species. *Archipheretima ophiodies* and *Planapheretima hasselti*, the male pores are on raised areas which extend onto *xviii–xx* and *xvii–xix* respectively (Figs 12a and 29b).

6 Female pores

The female pores are either paired or single, occurring ventrally on the equator of segment *xiv*. Occasionally individual variants may have paired female pores, although they belong to species in which the pore is usually single, the converse condition also occurs.

7 Genital markings

Glandular areas and other markings are present on the ventral surface of the anterior body wall of both clitellate and aclitellate individuals of many species. The nature and arrangement of these markings are specifically distinct and so provide valuable diagnostic information. They vary intraspecifically but these differences (degree of development and number of markings) may be attributed principally to growth since the patterns are usually constant in mature worms.

(*a*) *Diffuse genital markings* with poorly defined periphery are present only in the *Archipheretima iris* species-group where they are always intersegmental (Fig. 4a).

(*b*) *Discrete genital markings* with clearly defined periphera commonly occur in all of the genera revised below, they are usually segmental and only rarely intersegmental. These markings are usually circular or oval and differentiated into two or more concentric areas (large markings, Fig. 4b, small Fig. 4d); rarely, in *Polypheretima aringeana*, the central area of each genital marking is differentiated into small spots (Fig. 4e). The glandular tissue associated with the markings is usually restricted to the body wall, termed 'sessile' (Gates, 1972*a*). In species with very small markings, such as *grata*, the glandular tissue may invade the coelom in the form of a stalked gland. (In *grata* genital markings are present within the copulatory pouches but absent from the external, postclitellar ventral body surface.)

The genital markings on segment *xviii* are often similar in shape and position to those on adjacent segments, but they may be crescentic in shape and are closely associated with the male pores (Fig. 4c). Crescentic markings are present in *Metapheretima* (distinguishing the genus from *Polypheretima*), *Pleionogaster* and possibly two species of *Planapheretima* (*celebensis* and *moultoni*). Histologically crescentic markings are indistinguishable from the more common circular and oval genital markings.

(*c*) *Annular ridges* encircle the male pores in several species of *Metapheretima* (*orcrista*, *parmata*, *glamdringi*, *jocchana*) and one species of *Planapheretima* (*maculata*). Several other species of *Metapheretima*, all members of the *oinakensis* species-group, have similar, but less extensively developed structures. Functionally these structures would appear to facilitate the transfer of sperm between opposing male and spermathecal segments during copulation.

8 Septa

In the oesophageal and pharyngeal regions septa are often absent, incomplete or thickened. Considerable variation exists within a species and septal characters appear to be of little diagnostic value (especially in view of the imprecise terms 'delicate', 'membranous', 'thickened', etc., which are used in descriptions). The absence or incomplete development of the septa associated with the gizzard (8/9 and 9/10) and, when present, the oesophageal pouches (10/11 and 11/12) can be correlated with the degree of development of these organs. In *Pleionogaster*, in which the oesophageal gizzard is vestigial, the anterior septa are uniform.

The septal muscles form part of the musculature of the hydrostatic skeleton (Chapman, 1958). Thickened muscular septa may therefore be indicative of an active burrowing species, certainly the musculature is poorly developed in arboricolous forms whose functional requirements are different.

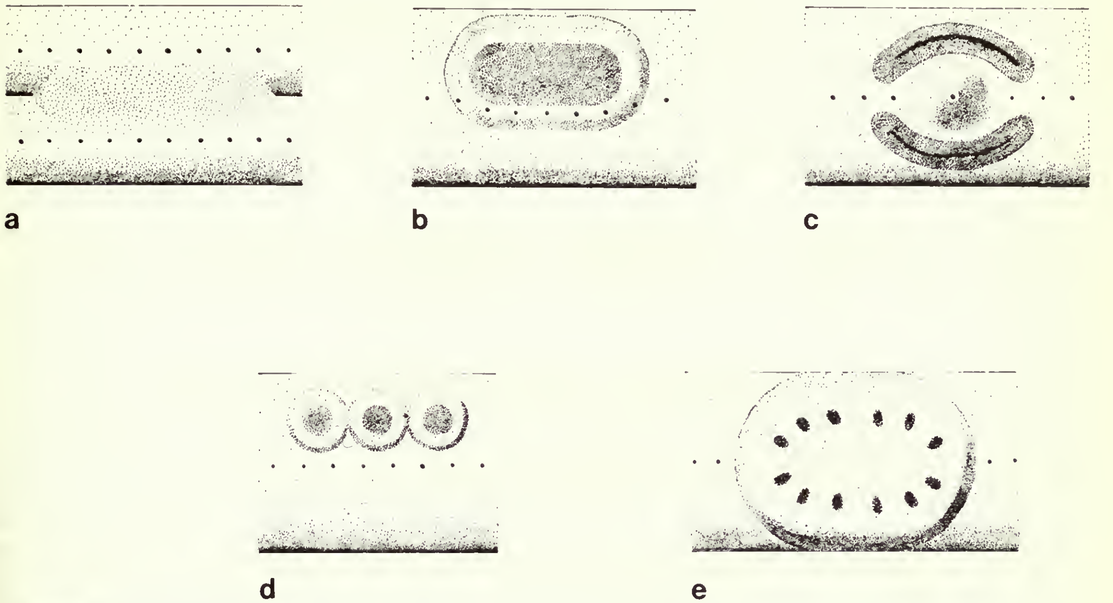

Fig. 4 Terminology of genital markings. (a) diffuse; (b) large discrete; (c) crescentic; (d) small discrete; (e) *Polypheretima aringeana* type.

9 Alimentary canal

Within the Megascolecidae (*sensu* Gates, 1959) the *Pheretima* group of genera is characterized by the presence of an oesophageal gizzard in *viii*. In most species the gizzard is well developed, invading the next two posteriad segments, but in the monotypic *Pleionogaster* it is vestigual and its function is taken over to some extent by the intestinal gizzards which characterize the genus. Oesophageal pounches, structures of unknown function, may be present in some species of *Metapheretima*. They are usually paired, flexed anteriorly, and arise from the dorsal surface of the oesophagus immediately posteriad to the gizzard. The extent of their development varies considerably among the series examined; they are often darkly pigmented and always have a well-developed blood supply.

Intestinal caeca are absent from most of the species investigated with the exception of a few Asian species of *Planapheretima*. In some of the latter and several related acaecate forms, the intestinal wall was reported as being glandular (Chen, 1946) but it has not been possible to examine material and the taxonomic significance of this specialization is uncertain.

10 Lateral hearts

Four pairs of circumoesophageal contractile blood vessels are usually present, one pair in each of *x–xiii*, although the posterior or anterior pair may be absent or incomplete. As the number of pairs often vary individually within a species, the differing conditions are of little taxonomic significance.

11 Anterior male reproductive system

The majority of species of the *Pheretima* group are holandric (testes paired in both *x* and *xi*) as are all of the known species of *Archipheretima*, *Planapheretima* and *Pleionogaster*. Species with a proandric condition (testes paired in *x* only) are rare and acaecate examples are accommodated in *Metapheretima* (with the possible exception of *sibogae* in *Polypheretima*). Metandric species (testes paired in *xi* only) occur in both *Polypheretima* and *Metapheretima*; in the former genus metandry is restricted to (and diagnostic of) members of the *badia* and *patae* species-groups. However, in *Metapheretima* the character has a limited taxonomic value since metandry is present in most of the species-groups recognized.

With the possible exception of several species of *Archipheretima*, the testes are invested by tough membranous sacs in all species of the *Pheretima* group, including *Polypheretima fida*, although testes sacs were recorded as being absent in this species (Michaelsen, 1913*b*; Stephenson, 1930). In *Archipheretima* the sacs are usually more delicate and larger, mostly forming a lining to the parietal wall, although they have been reported as absent in some species (Gates, 1970*a*). The shape and the extent of the testes sacs varies with genus, species and to some extent with the maturity of an individual. In a few species the seminal vesicles and lateral hearts may also be enclosed within the testes sacs.

The seminal vesicles are paired, posteriorly directed, sac-like evaginations of the hinder septa of each testes segment. In most species each pair is restricted to one segment where their size varies with maturity, but in several Chinese species of *Planapheretima*, they extend several segments anteriorly and posteriorly.

Small, paired sacs which resemble the seminal vesicles may be present on the posterior surfaces of septa 12/13 and 13/14. These structures of unknown function have been termed *ovisacs* (Beddard, 1895), *coelomic sacs* (Sims & Easton, 1972) and *pseudoseminal vesicles* (Gates, 1972*a*). It is proposed here to adopt the term *pseudoseminal vesicles*, to avoid confusion with other structures described as *coelomic pouches* and *coelomic sacs* by Beddard & Fedarb (1902).

12 Ovaries

The female gonads are paired and free in *xiii* in all the species investigated as well as the majority of other species of the *Pheretima* group. However, the ovaries are enclosed in delicate walled sacs in *Pithemera mira* and several related taxa from New Britain and nearby islands (Gates, 1972*b*).

13 Spermathecae

The duct and ampulla of each spermatheca are distinctly demarcated in mature individuals of most of the species reviewed here. In immature specimens, and mature examples of *Archipheretima*, the duct merges gradually into the ampulla. In species of the acaecate genera a diverticulum (rarely several diverticula) arises from the spermathecal duct and provides a useful diagnostic character for generic, species-group and specific identifications. Several types of diverticula are encountered (Fig. 5).

The spermathecal pores may be either small (and difficult to see) or large, often within tumid lips. Gates (1972*a* : 150) described the large spermathecal pore as secondary since he recognized a minute (primary) pore within the invagination. The taxonomic aspect of this specialization was not investigated during the present study.

The number and situation of spermathecae may vary within a thecal segment. These variations are reflected in the arrangement and number of spermathecal pores which are often diagnostic of species-groups and species. The pores may be segmental as in *Polypheretima annulata* and *P. voeltzkowi* or, more usually, intersegmental. In both situations they occur either in a single furrow, or segment, or in several consecutive furrows between 4/5 and 8/9, even 7/8/9/10 in the case of *Metaphire sanseiana* (Ohfuchi, 1951). When monothecate there is a single pore either dorsally or ventrally placed in each segment (a single lateral pore indicates an abnormal example of a bithecate species). Bithecate species have two symmetrically placed pores, while numerous pores arranged in paired symmetrically placed batteries are external evidence of polythecate species. Most species are monothecate, bithecate or polythecate but some may be divided, being, for example, bithecal in some segments and polythecal in others. Immature specimens of polythecal species may be bithecal while the number of spermathecae in the batteries of the species of the *Polypheretima elongata* species-complex increases with maturity (Easton, 1976).

In bithecal and polythecal species the ventral separation of the pores (or batteries) can be expressed as a fraction of the body circumference at that segment. This proportion is reasonably constant in a taxon and often diagnostic. In this paper the separation of the most posterior spermathecal pores is utilized since occasionally the more anterior pores are more closely paired.

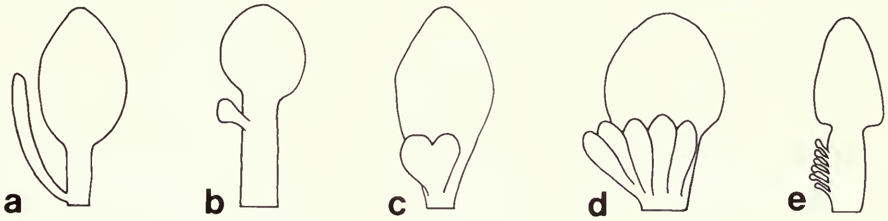

Fig. 5 Spermathecae. (a) differentiated with simple ectal diverticulum; (b) differentiated with simple ental diverticulum; (c) undifferentiated with multilocular diverticulum (*Archipheretima*); (d) differentiated with multilocular diverticulum (*Metapheretima*); (e) differentiated with numerous diverticula.

14 Nephridia

The nephridia were excluded from the present numerical and taxonomic investigations due to the uncertainty about their systematic significance (see Classification) and for much the same reasons that they were omitted by Sims & Easton (1972). The study of the nephridia would necessitate the destructive dissection of well-preserved specimens, and it was clearly undesirable to go to such extreme lengths to obtain information. Secondly, some species are represented by specimens often in poor condition due to either inadequate fixation, or previous dissections, so that information can no longer be obtained from them. Only a minority of the original descriptions include details of the nephridial system, so that it would be difficult to correlate this information.

Nevertheless, variations in the nephridial system of a few species were studied for other reasons since, in the most recent classification of the Megascolecoid earthworms, Jamieson (1971*a* & *b*) attributed considerable systematic importance to the structures of the excretory systems (see Classification).

Numerical studies

Introduction

Since only 14 acaecate species were assessed in the numerical investigations of Sims & Easton (1972), it was decided to subject the majority of the 92 species recognized here to a fuller numerical appraisal. The taxa selected for study and the characters assessed are listed in Tables 1 and 2 respectively. The data utilized was extracted from the specific descriptions in the taxonomic section of this paper, instead of from the examination of a single individual which has been the practice of earlier authors. The techniques used resemble those employed by Sims & Easton (1972) but the analyses were performed with the aid of a program adapted from the CLASP computer program (Gower & Ross, Rothamsted Experimental Station) for use with the Varian V72 computer in the British Museum (Natural History). The mutual similarity coefficients of the taxa investigated were calculated using a coefficient of similarity defined for both quantitative and qualitative characters. A two-dimensional plot of the taxa involved was obtained using the method of principal co-ordinates analysis and a Minimum Spanning Tree (MST) was added to the plot.

Table 1 List of taxa studied in numerical investigations

Archipheretima
1 *iris*
2 *margaritacea*
3 *mazarredi*
4 *zonata*
5 *ophiodes*
6 *picta*

Metapheretima
7 *arensi*
8 *bulmeri*
9 *carolinensis*
10 *elrondi*
11 *pallens*
12 *pickfordi**
13 *queribunda**
14 *quinqueremis*
15 *sembaluensis*
16 *sentanensis*
17 *simsi**
18 *sola*
19 *speiseri*
20 *triciae*
21 *trukensis*
22 *loriae*
23 *neoguinensis*
24 *septocta*
25 *sucklingensis*
26 *durendali*
27 *excalaberi*
28 *andurili*
29 *dorii*
30 *glamdringi*
31 *kilii**
32 *oinakensis*
33 *orcrista*
34 *parmata**
35 *stingi*
36 *jocchana*

Polypheretima
37 *annulata*
38 *fakfakensis*
39 *bifaria*
40 *brevis*
41 *fida*
42 *gatesi*
43 *iizukai*
44 *mertoni*
45 *monticola*
46 *panarana*
47 *sempolensis*
48 *sepikensis*
49 *taprobanae*
50 *grata*
51 *voeltzkowi*
52 *annamensis*
53 *aringeana*
54 *elongata*
55 *everetti**
56 *kinabaluensis**
57 *phacellotheca*
58 *stelleri*
59 *koyana*
60 *lesonea*
61 *pentacystis*
62 *polytheca**
63 *renschi*
64 *badia*
65 *elberti*
66 *kellneri*
67 *swelaensis*
68 *sibogae*
69 *coplandi**
70 *kershawae*
71 *patae*

Planapheretima
72 *continens*
73 *lacertina*
74 *tenebrica*
75 *bambophila*
76 *arboricola*
77 *celebensis*
78 *moultoni*
79 *pallescens*
80 *rufomaculata*
81 *subulata*
82 *ambulatrix*
83 *hasselti*
84 *maculata*
85 *nieuwenhuisi*

Pleionogaster
86 *horsti*

* Species not included in the initial numerical study.

Four separate numerical investigations were made. Firstly, a general study was undertaken to re-appraise the 'acaecate' genera recognized by Sims & Easton (1972). One result of this study was that *Ephemitra* is merged with *Metapheretima*, which is itself restricted, and the excluded species are here accommodated in *Polypheretima*. Then followed independent studies of each of the genera *Metapheretima*, *Planapheretima* and *Polypheretima* to detect the phenetic inter-relationships of their component species. Comparable information on the small genus *Archipheretima* is obtainable from the initial, general computations while *Pleionogaster* is monotypic. The results of these studies are discussed under each genus in the taxonomic section.

General Study

Seventy-eight species were utilized to provide data for the re-appraisal of the genera recognized by Sims & Easton (1972). It was not possible to include all of the species listed in Table 1 because of the limited capacity of the computer program employed, the taxa marked by an asterisk were those excluded from this study.

The configuration of the taxa with the first and second vectors of the principal co-ordinates analysis as axes is shown in Fig. 6. A considerable degree of clustering is evident, which becomes clearer with the addition of the Minimum Spanning Tree (MST) with graded linkages. Four major clusters may be recognized. Two, indicated by square and triangular symbols, comprise the six species of *Archipheretima* and 14 species of *Planapheretima* respectively, which by their discreteness and the low values of the MST linkages with other clusters confirm the validities of the genera. The two other clusters, indicated by closed and open circular symbols contain the taxa previously assigned to *Metapheretima* by Sims & Easton (1972). The species identified by closed circular symbols have male pores which lack porophores but usually have crescentic markings associated with them. The male pores sometimes discharge from within copulatory pouches when they are on elongate penes. The taxa principally from the Papuan region, have diverse types of spermathecal diverticula and genital markings which are usually in longitudinal rows. Included in this cluster are the type species of *Metapheretima* Michaelsen, 1928 and *Ephemitra* Sims & Easton, 1972. The taxa indicated by open circular symbols have the male pores on porophores which lack associated crescentic markings. These male pores sometimes discharge into copulatory pouches when the porophore forms a short truncate penis. The taxa, which come from all parts of the *Pheretima* group domain, always have simple spermathecal diverticula, but together exhibit a wide diversity of patterns of genital markings. The type species of *Polypheretima* is included in this cluster. The degree of separation of the clusters and the evidence of the MST linkages permit the recognition of two distinct genera *Metapheretima* and *Polypheretima*.

Table 2 Characters used for computing coefficients of similarity

1 Mean longitude
2 Mean latitude
3 Ratio of lengths of arcs containing first five dorsal setae (*v–z*): first five ventral setae (*a–e*) on segment *vii*
4 Shape of body in cross-section: circular or depressed
5 Creeping sole: present or absent
6 Segment number of anterior end of clitellum
7 Segment number of posterior end of clitellum
8 Size of spermathecal pores: large or small
9 Ratio of distance apart of posteriormost spermathecal pores: circumference of body
10 Position (furrow number) of anteriormost spermathecal pores (one 'furrow' = setal row – setal row)
11 Position (furrow number) of posteriormost spermathecal pores
12 Position of spermathecal pores: postsetal, intersegmental, or presetal
13 Main number of spermathecal pores per furrow
14 Origin of spermathecal diverticula: ectal or ental
15 Condition of spermathecal diverticula: single or multiple
16 Condition of male pores: crescentic copulatory pouches, slightly invaginated porophore, superficial porophore, superficial lacking porophore, penate simple or penate within copulatory pouches
17 Size of male pore (superficial lacking porophore only): large or small
18 Ratio of distance apart of male pores: circumference of body
19 Annular ridges associated with male pores: absent or present
20 Crescentic markings associated with male pores: absent or present
21 Form of genital markings: diffuse or discrete
22 Postclitellar genital markings (discrete only) number on each segment
23 Glands associated with genital markings: sessile or stalked (discrete only)
24 Oesophagus: simple, slightly pouched, or distinctly pouched
25 Intestine: caecate, simple, with gizzards
26 Intestinal wall: unspecialized or glandular
27 Number of first intestinal segment
28 Condition of testes: proandric, holandric or metandric
29 Condition of testes sacs: absent, large membranous, annular, large paired, small paired

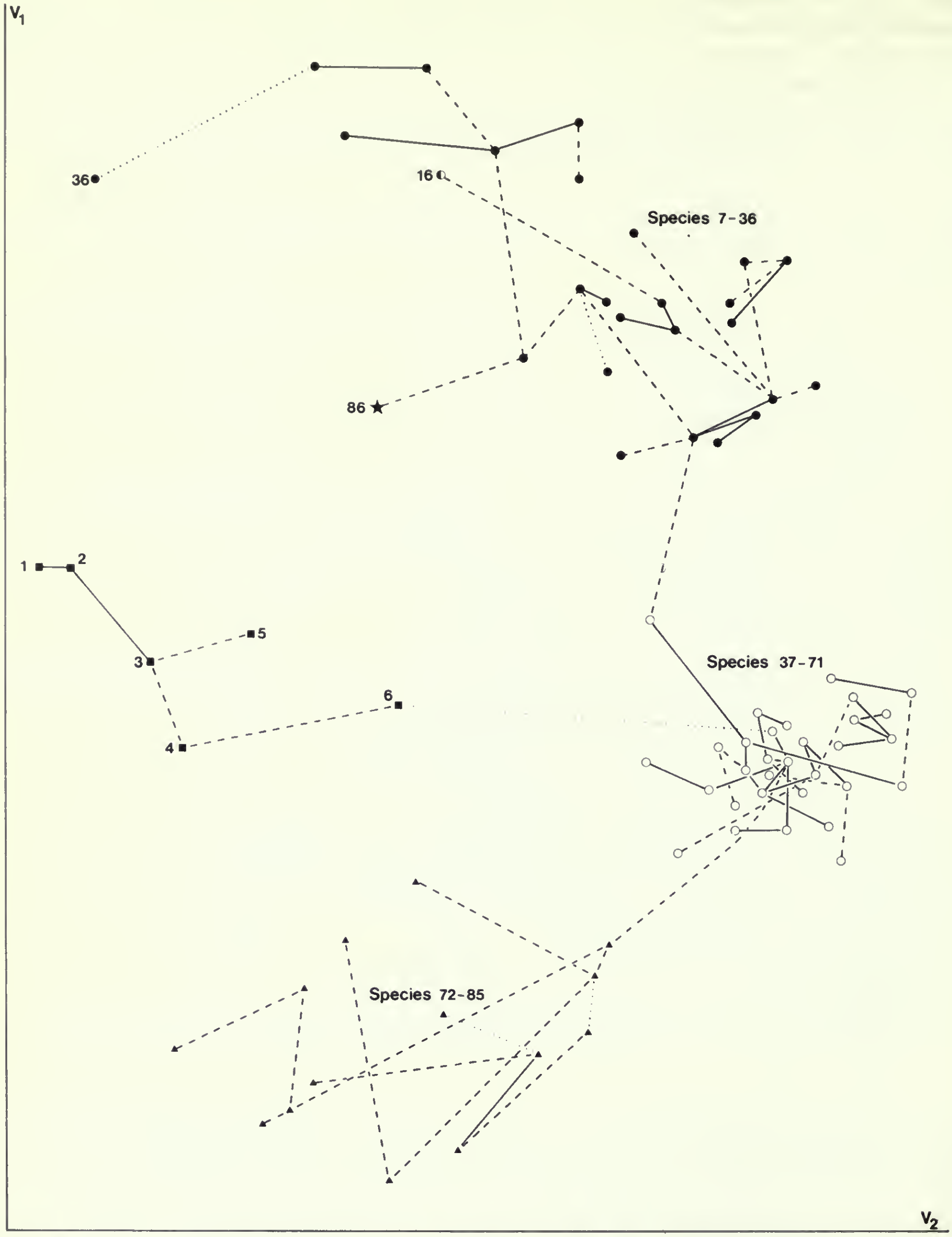

Fig. 6 Principal co-ordinates analysis of 78 'acaecate' species: the configuration of the species with the vectors corresponding to the first and a second latent roots. The linkages of the added Minimum Spanning Tree are graded to indicate percentage similarities; ——, +95%; - - - - -, 90–95%; · · · · ·, −90%. The genera recognized are depicted thus: *Pleionogaster* – star-shaped symbol; *Metapheretima* – closed circular symbols; *Polypheretima* – open circular symbols; *Archipheretima* – square symbols; *Planapheretima* – triangular symbols.

The species *horsti*, represented by a star in Fig. 6, is linked by the MST to *Metapheretima* (indicated by closed circular symbols) at 90·0% similarity. This value is higher than many of the MST linkages within *Metapheretima* and the locus of *horsti* is closer to the centre of the cluster than several taxa of *Metapheretima*, notably *jocchana* (36). Nevertheless, *horsti* is the type species and only representative of the genus *Pleionogaster* which is unique among the Megascolecidae in possessing intestinal gizzards. Since this character is not only unique but also considered by most workers to be of considerable systematic importance, it is proposed to retain this genus as a separate entity.

Except for these changes, the numerical results are in accord with those of Sims & Easton (1972), when a dissimilar set of morphological attributes were coded and processed on a larger computer. These authors indicated that the species accommodated here in *Polypheretima* could be distinguished from other acaecate forms, but they were uncertain of the taxonomic significance of the diagnostic characters of this group, and refrained from separating the species taxonomically.

Distribution

The distribution of the acaecate members of the *Pheretima*-group of genera need to be discussed in the context of the indigenous ranges of all the species within the group. Moreover, assessments of the affinities and origin(s) of the individual pheretimoids need to be considered in the light of the wider distribution of the group as a whole.

The *Pheretima* group domain

The concept of the *Pheretima* group domain, the area in which all of the autochthonous species of the *Pheretima*-group of genera occur (Fig. 7), was pioneered by Michaelsen (1903*b*, 1908, 1928*b*). In the last work the area was defined as comprising Japan, China, Burma through southeast Asia and the Indo-Australasian Archipelago to Queensland then to New Caledonia, the New Hebrides, the Caroline Islands and, tentatively, the Comoro Islands. The results of recent collecting now make it possible to establish most of the boundaries with greater precision. The northern limit is bounded by the most northerly records of *Metaphire aggera* (Kobayashi, 1934) which form a line linking Chihfeng, Yamhsin (Chinhsein) and Tashihkiano (Tashihchiano) in Manchuria with P'yongyang (Heijo) and Kumgang-san (Mt Kongo) in Korea (Kobayashi, 1940). In the west, Chen (1931, 1936, 1946) recorded a rich indigenous fauna from Szechwan Province while Gates (1972*a* : 149) recognized that the Chindwin–Irrawaddy axis marked the westerly limit of the domain in Burma. In the south only a single indigenous representative of the *Pheretima* group, *Amynthas queenslandicus* (Fletcher, 1887), has been recorded from Australia since *enchytraeoides* Michaelsen, 1916, also from Queensland, was shown by Gates (1961) to be a synonym of the peregrine species *A. minimus* (Horst, 1893). Expeditions organized by Dr B. G. M. Jamieson have collected several new indigenous species in northern Queensland, although only peregrine species were found in Northern Territory (Easton, in prep.). It seems certain, therefore, that much of the tropical forest of Queensland belongs to the domain. The precise eastern limit of the domain is uncertain, since several species have ranges which include Pacific islands. Species have been described from the Marianas, Caroline Islands, Solomon Islands, New Hebrides and Loyalty Islands, which have not been encountered in other parts of the domain and it seems reasonable to to follow Michaelsen (1928*b*) and include at least these islands within the realm. The Comoro Islands also possess a species of the *Pheretima* group which does not occur elsewhere. Although Michaelsen (1928*b*) included the Comoro Islands within the domain, in view of the evidence discussed below, these islands are here excluded.

It is evident that the *Pheretima* group domain extends throughout the forested lands of Asia and Australasia, but it is curiously restricted in some areas. In the north and northwest the limiting factors are apparently climatic. In Korea and Manchuria the northern boundary coincides with the 8° isotherm (annual mean temperature), and in Manchuria the western limit of the domain is marked by the 400 mm isohyet (Kobayashi, 1940). It is possible that isolated populations may occur in moist refuges to the west of the 400 mm isohyet since it has been suggested (Wadia, 1960) that the dessication of central Asia is a post-glacial phenomenon. To the southwest the 400 mm

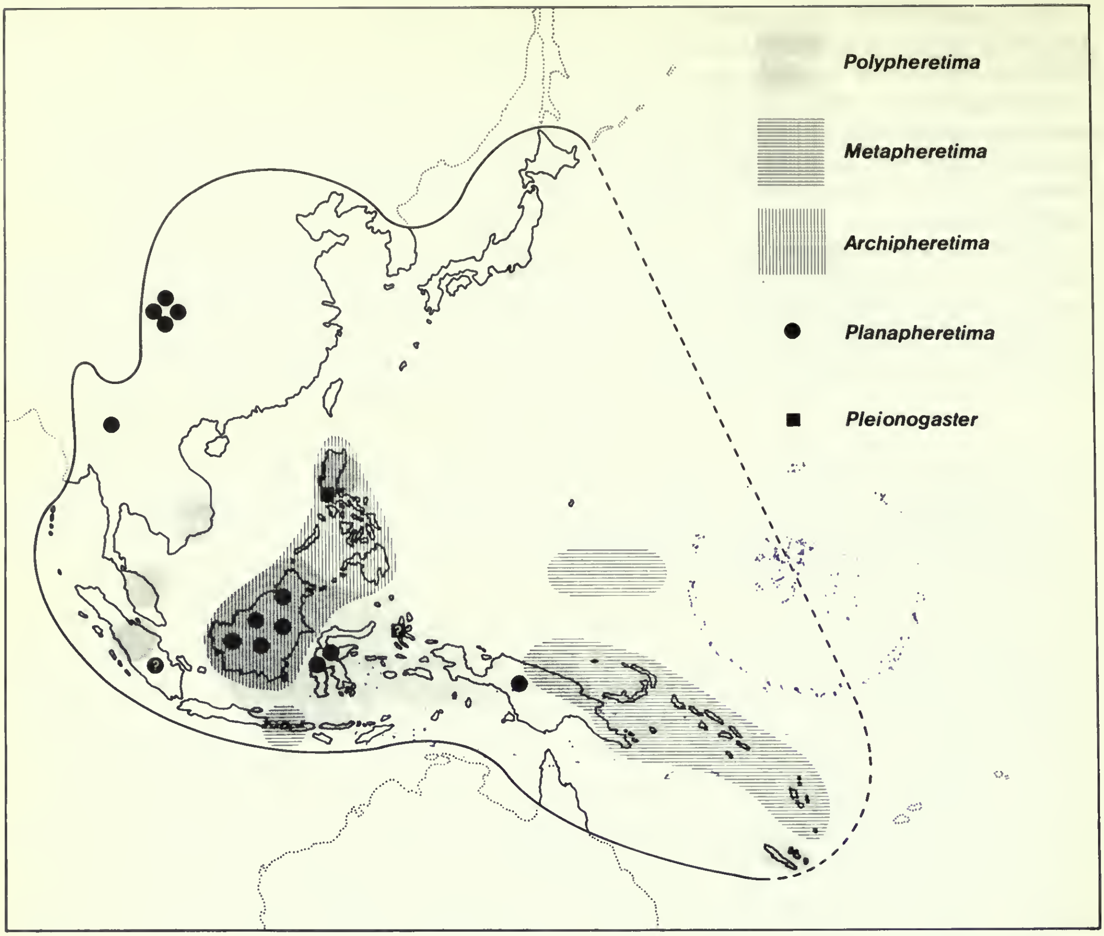

Fig. 7 Geographical limits of the *Pheretima* group domain and the distribution of the acaecate genera.

isohyet enters the Himalayas, where low precipitation and temperature provide a major barrier to earthworm migration.

Further south there are neither rainfall nor temperature barriers of any significance which may be correlated with limits of the *Pheretima* group. Nevertheless, a discrete boundary can be seen to exist and here it is necessary to examine the Caenozoic palaeogeography of Asia and Peninsula India to understand the pattern of distribution. During the Mesozoic when the Tethys ocean separated Peninsula India from Asia the direct interchange of earthworm faunae was not possible. In the Tertiary era conditions changed and the Indian and Asian plates approached their present relative positions. Western Burma and Bangladesh remained a barrier to earthworm migrations, since the Cretaceous and Tertiary sediments in this area did not become land to any great extent until the end of the Pliocene (1·5–3·5 million years ago) (Wadia, 1953). In Burma proper, although the ridges of the Chin hills/Araken Yoma and Pegu Yoma were formed during the Eocene and Miocene respectively, the intervening valleys remained below sea level even during the Pliocene (Krishnan, 1952). When the land links were eventually established the *Pheretima* group could have invaded Peninsula India from the east, but only the more successful peregrine species apparently did so. These occur nowadays throughout much of southern India and they may have attained this distribution unaided but in view of their occurrence on other continents it is likely that they were assisted adventitiously by man. Most of the non-peregrine species of this area remain confined to the east of the Chindwin–Irrawaddy axis. This faunal limit lies between 100 and 150 km west of a line from the Irrawaddy south to Mandalay to the foot of the Shan plateau to the Sittang valley, i.e. the boundary of the Asian archean rocks (Rao, 1974 : 238).

In Australia the limiting factors forming the southern boundary of the *Pheretima* group domain are not known precisely but they appear to be largely ecological.

As most Megascolecoidea (Megascolecidae *sensu* Jamieson, 1971*a* and Eudrilidae) are indigenous on land masses which once formed part of Gondwanaland, it seems likely that they evolved in this region and that their precursors existed in Gondwanaland prior to the Mesozoic break up of this ancient continent. The presence of the *Pheretima* group and other Megascolecid species in southeast Asia and the occurrence of several genera in North America, is probably due to invasions of these Laurasian land masses from the widely dispersed fragments of Gondwanaland. In this model of Megascolecoid dispersal, the origin of the *Pheretima* group would lie in New Guinea and northern Australia since these are the only major Gondwanaland derived areas inhabited by indigeneous species. The invasion of Asia by way of the Indo-Australasian Archipelago could therefore have followed the collision of the Australian and Asian Plates during the Miocene, 7–26 million years ago (Raven & Axelrod, 1972).

If the primordial pheretimoids had emerged before the Mesozoic breakup of Gondwanaland, it would have been possible for them to have migrated westwards to other regions and give rise to the species suspected of being indigenous in the Comoro Islands. However, the absence of any surviving indigenous species in the intervening areas, and the paucity of the *Pheretima* group in the Malagasian fauna, makes this seem unlikely. Emigration may have occurred eastwards to the Solomon Islands, New Hebrides and New Caledonia which, prior to 80 million years ago, were juxtaposed to Queensland (Griffiths, 1971). It should be noted, however, that today the *Pheretima* group is not indigenous in New Zealand although these islands too rifted from the eastern margin of the Australian Plate at that time. Other mechanisms by which earthworms may have colonized oceanic islands were discussed by Stephenson (1930).

Distribution of the 'acaecate' pheretimoids

The individual acaecate genera, although often sympatric, have dissimilar ranges (Fig. 7). *Archipheretima* is restricted to Borneo and the Philippines while the genera *Polypheretima* and *Planapheretima* are the most widespread, occurring throughout the Indo-Australasian archipelago to the northern and western limits of the *Pheretima* group domain. In Asia, they are now restricted to isolated refuges so presumably they were once continuously distributed throughout the area. *Metapheretima* is restricted principally to New Guinea, where it is the commonest acaecate pheretimoid. The monotypic genus *Pleionogaster*, closely allied to *Metapheretima* (see numerical studies) and probably a product of the *Metapheretima* radiation, is recorded only from the Philippines and possibly the Moluccas. The genera *Polypheretima*, *Planapheretima* and *Metapheretima* probably represent three radiations from the Papuan area.

The species-groups comprising the genus *Metapheretima* are largely sympatric and there is seemingly insufficient evidence to recognize any evolutionary patterns among them. Similarly, the ranges and morphological variation of the species of *Archipheretima* are too poorly known to permit valid conclusions to be drawn.

The infra-generic assemblages recognized within *Polypheretima* are, on the other hand, mainly allopatric and when their ranges are considered together with their morphological variations, the information provides a means of tracing the probable evolution of the genus. The species-groups of *Polypheretima* (see taxonomy section) form a series in which the morphological specializations increase as the geographical ranges decrease (Fig. 8). The most widespread, the *bifaria* species-group (Division I), is holandric with simple male pores (the species *grata*, *voeltzkowi* and the *annulata* species-complex, also members of Division I, are considered to be local specializations); the *polytheca* species-group (Division II) is similarly holandric but the male pores open within copulatory pouches; while the most restricted in their distributions, the *badia* and *patae* species-groups (Division III), not only have male pores within copulatory pouches but also they are metandric. Although the *badia* and *patae* species-groups apparently have high mutual affinities (see Taxonomy section), in view of their widely separated ranges, it is probable that they have developed metandry independently. Possibly the *bifaria*, *polytheca*, *badia* and *patae* species-groups represent successive radiations which occurred in different parts of the range of *Polypheretima.* These radiations are probably of considerable antiquity since the ranges of the species-groups cannot be correlated with either Wallace's or Weber lines. Two species for example, *P. elongata* and *everetti*, even occur on both sides of Wallaces line.

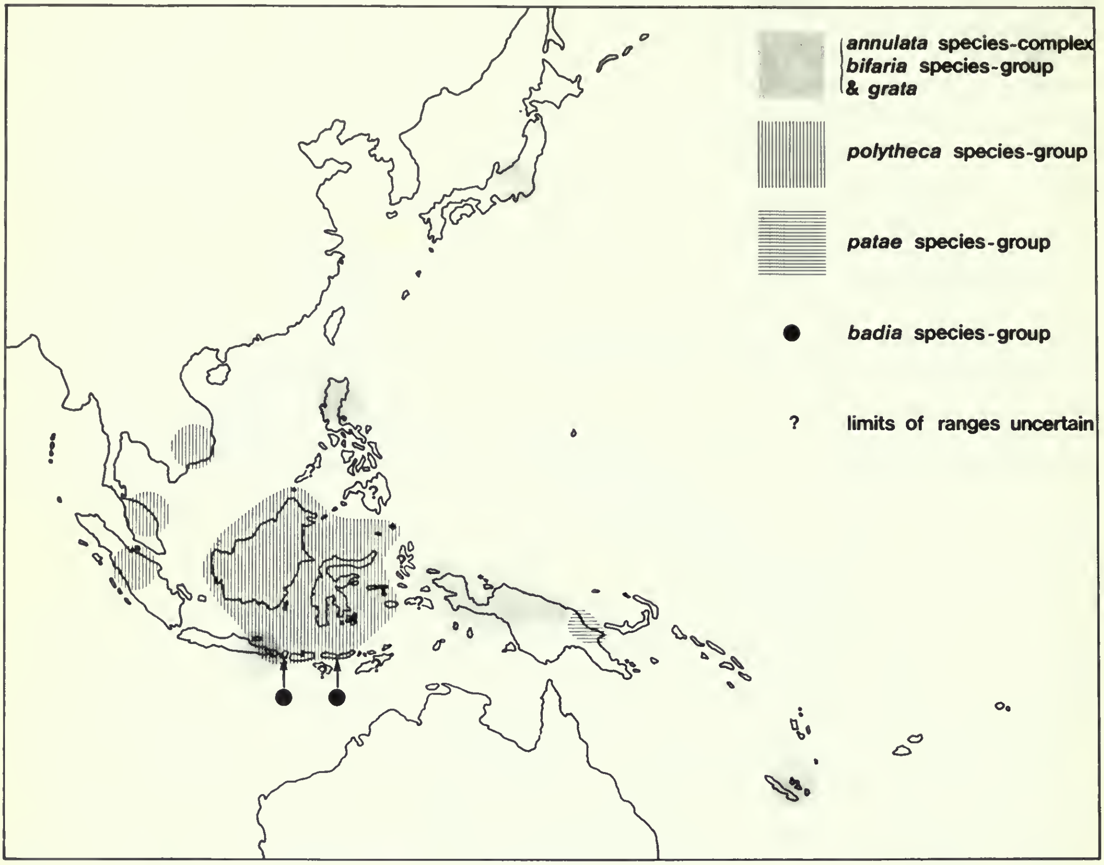

Fig. 8 *Polypheretima*: geographical distribution of the component species-groups.

The two divisions of *Planapheretima* are also allopatric. Species of Division I have unspecialized intestines and occur in the Indo-Australasian archipelago while those of Division II have specialized intestines and are indigenous to the Asian mainland. Probably precursors of Division II had simple intestines but whether this group arose in Asia is more speculative (see taxonomy section).

In the northwestern and southeastern limits of the *Pheretima* group domain the acaecate genera occur only sporadically in isolated refuges, here the *Pheretima* group is represented mainly by the caecate genera *Amynthas*, *Metaphire* and *Pheretima* s.s. Many of the Asian species of *Amynthas* and *Metaphire* differ from species of *Polypheretima* only in the possession of intestinal caecae while most of the Papuan and Australian species of *Amynthas* may be considered to be caecate analogues of *Metapheretima*. Since the possession of intestinal caeca is a specialization, the caecate species may have emerged independently more than once, possibly from this acaecate stock and have replaced them in the northwestern and southeastern parts of the domain.

Classification

For some time the opinion has been often held that 'the key to the classification of the . . . (terrestrial oligochaeta) is to be found in the modifications of the excretory system' (Beddard, 1890*b*). The result is that the structure of the nephridial system has played an increasingly important part in earthworm classifications, although its application often has been hampered by the paucity of available information. During the last two decades several disparate classifications of Megascolecoid earthworms have been proposed (Omodeo, 1958; Gates, 1959; Lee, 1959; Jamieson, 1971*a* & *b*). In the latest Jamieson divided the Megascolecinae, which includes the *Pheretima* group of genera, into three tribes. The tribes Dichogastrini and Megascolecini both include genera with combined male and prostatic pores, and a meronephridial excretory system. In genera assigned to the former tribe the median nephridia are exonephric; while in those of the latter tribe, median nephrida are enteronephric or absent. Enteronephridia have been recorded from no more than five species of the *Pheretima* group of genera; *Metaphire posthuma* by Bahl (1919), *Amynthas hupiensis* by Grant (1955), tentatively in *Pleionogaster horsti* by Gates (1943) and possibly in *Amynthas hawayanus* and *A. diffringens* by Bahl (1919) although the identities of the specimens representing these species have been questioned (Gates, 1937*b*). Jamieson (1971*a*) accepted Bahl's (1946) syllogism that since a few species of *Pheretima* possess enteronephridia so all members of the genus (now the *Pheretima* group of genera) have them too, therefore he assigned the group to the enteronephric tribe Megascolecini.

Due to the importance accredited to the structure of the nephridial system and the paucity of data available for most species of the *Pheretima* group, the nephridial systems of examples of the acaecate genera were examined. Comparisons were made with the description of Bahl (1919) who recognized three types of nephridia in *M. posthuma*.

1. Tufted nephridia, present in the segments anterior to the gizzard and discharging into the pharynx.

2. Body wall nephridia, present in all segments except *i*. These are numerous, Bahl recorded 200–250 in a segment and Grant (1955) reported 175 in each segment in *A. hupiensis*. Bahl reported that in *M. posthuma* each nephridium discharged independently but Beddard (1888) stated that in *A. hawayanus* each nephridium was linked by a reticulum to other nephridia, both of its own and of adjacent segments. [It should be noted that Beddard (1888) provisionally identified the specimens as *aspergillum* but later (1895 : 43) he established that they were *bermudensis* = *hawayanus*.] Spencer (1888) reported a similar nephridial reticulum in *Megascolides australis*.

3. Median nephridia, present on septum 15/16 and posteriorly to the end of the body. Eighty to one hundred nephridia are present on the anterior and posterior surfaces of each septum in *M. posthuma* and 70–80 in the case of *A. hupiensis* (Grant, 1955). In both species, the nephridia are enteronephric in that they are linked by paired, postseptal ducts which run dorsally and medianly to discharge into paired supraintestinal ducts, these in turn discharge, at intervals, into the intestine.

In this present study, examples of two species, *Metapheretima sentanensis* and *Polypheretima taprobanae*, were examined in detail and examples of four other species, *M. neoguinensis* (type species of *Metapheretima*), *P. stelleri* (type species of *Polypheretima*), *P. elongata* and *Pleionogaster horsti* (=*jagori*, type species of *Pleionogaster*) were compared with them. The specimens examined had been preserved in alcohol for several years prior to study, so they were stained with methylene blue to enhance the recognition of the decolourized internal structures. Modifications and variations were found in each of the three types of nephridia described above among the species examined (Table 3).

1. Tufted nephridia are present in *iv–vi* in all of the species examined. The nephridia occur as paired lateral masses on the peripheries of the anterior surface of the septa and paired excretory (?) ducts can be traced passing between each nephridial mass and the pharyngeal mass. Additional tufted nephridia are present in *vii* and *viii* in *neoguinensis* and in *vii–ix* in *horsti* and *sentanensis*. When the posterior septa of these segments are absent or incomplete the nephridia form paired lateral bands on the body wall. In *sentanensis* paired excretory (?) ducts can be traced passing from

Table 3 Summary of nephridial types in selected species of the *Pheretima* group

Nephridial types		*Metaphire posthuma* (data from Bahl, 1919)	*Metapheretima sentanensis*	*Metapheretima neoguinensis*	*Pleionogaster horsti*	*Polypheretima taprobanae*	*Polypheretima elongata* and *stelleri*
Tufted Nephridia	discharging into pharynx	*iv–vi*	*iv–vi*	*iv–vi*	*iv–vi*	*iv–vi*	*iv–vi*
	discharging through body wall	–	*vii–ix*	*vii–viii*	*vii–ix*	–	–
Body wall Nephridia	simple	*ii*–pygomere (*c.* 200/seg)	*x–cx* (*c.* 40/seg)	*vii*–pygomere	*x*–pygomere (*c.* 10/seg)	*vii–xc*	*iv*–pygomere
	with semi-annular sinuses	–	*cx*–pygomere	–	–	*xc*–pygomere	–
Median Nephridia	presetal	15/16–pygomere (*c.* 50/septa)	43/44(2)–70/71(40)–90/91(10) sparse on following septa	18/19–pygomere	18/19–pygomere (1 pair/septa)	15/16–pygomere	sparse
	postsetal	15/16–pygomere (*c.* 50/septa)	as presetal but only 10/septa at 70/71	18/19–pygomere	–	–	–
	excretory ducts	enteronephric	not recognized	not recognized	not recognized	not recognized	exonephric

the nephridial masses of *vii* and *viii* forward to enter the body wall in the vicinity of the spermathecal pores. In *xi* where each lateral band is subdivided into three discrete masses, no ducts can be recognized. Gates (1943) first described the tufted nephridia of *vii–ix* in *horsti* and similar structures have been recognized in several species of *Lampito* (Bahl, 1924) and *Megascolex* (Vata, 1945).

2. Body wall nephridia vary in number according to the species and the region of the body studied, they are however always absent from the anteriormost segments. In *horsti* and *sentanensis* they are particularly sparse (*c.* 10 and *c.* 20 per segment respectively). The external nephridiopores described by Beddard (1888) and Bahl (1919) cannot be recognized. The reticulum described by Beddard (1888) appears to be present although transverse microsections need to be studied to confirm this observation.

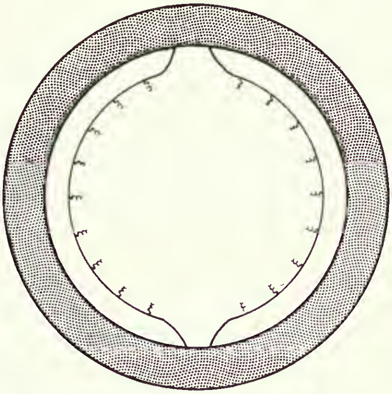

Fig. 9 *Metapheretima sentanensis*: schematic diagram of a transverse section through the equatorial region of a posterior segment showing the semiannular sinuses and associated nephridia.

In the posteriormost segments of two of the specimens examined (*sentanensis* and *taprobanae*) the body wall nephridia of each segment apparently discharge into a pair of semi-annular lateral sinuses (Fig. 9). Excretory ducts leading to external pores are apparently absent. These structures may be analogous to the coelomic pouches of *M. posthuma* described by Beddard & Fedarb (1902), but it is possible that they are artifacts resulting from the epithelial lining of the coelom becoming detached during fixation or preservation.

3. Median nephridia are present in all of the species studied, but their numbers and positions vary from species to species. In *elongata* and *stelleri* they are sparse and close to the body wall and are apparently linked to the reticulum of the body wall nephridia. In *horsti* a single pair of large nephridia with preseptal funnels are present from septum 18/19 and Gates (1943) tentatively recognized a pair of postseptal excretory ducts leading to the dorsal portion of the intestine in each segment. In *taprobanae* there are numerous nephridia with preseptal funnels on each septum from 15/16 to the posterior end of the body. They lie in paired lateral arcs approximately halfway between the intestine and the body wall. In *sentanensis* a single pair of nephridia with preseptal funnels are present on septum 43/44, but the number of nephridia increase posteriorly to septum 70/71 where there are about 40 with preseptal funnels and 20 with postseptal funnels. The nephridia then decrease in number until septum 90/91 where there are about 10 with preseptal funnels and only two or three with postseptal funnels. Where they are reduced in number, the nephridia are dorsally situated. In *neoguinensis*, the nephridia are close to the periphery of each septum, occurring regularly through the body from septum 18/19.

Discussion

From this brief morphological survey it emerges that the nephridial systems of the species examined differ considerably, although they all possess median nephridia. Enteronephric ducts.

diagnostic of the Megascolecini (Jamieson, 1971*a* & *b*) and recorded in *Metaphire posthuma* by Bahl (1919) and *Amynthas hupiensis* by Grant (1955), could not be identified in any of the species studied although exonephric ducts, diagnostic of the Dichogastrini (Jamieson, 1971*a* & *b*), appear to be present in *Polypheretima elongata* and *P. stelleri.*

As nephridial structures characteristic of two of these different tribes are present within the homogeneous assemblage of species forming the *Pheretima* group of genera, it seems that these structures are unreliable characters for higher classification. If they were accepted, then members of the *Pheretima* group would be distributed between the Dichogastrini and the Megascolecini. Clearly this would be unacceptable. Until new taxonomic criteria can be recognized, or evidence conflicting with the results of the phenetic study become available, it is intended to revert to the older classification of Megascolecoid earthworms proposed by Gates (1959) within which the *Pheretima* group can be more readily accommodated.

The Megascolecidae (Gates, 1959) – 'species with racemose prostates of the *Pheretima* type, without a central lumen and presumably of mesodermal origin' – includes the *Pheretima* group of genera (*c.* 760 nominal species) and about thirteen other genera with approximately 280 species. Similarly, the tribe Megascolecini Jamieson, 1971*a* & *b* accommodated ten genera containing about 210 species in addition to the *Pheretima* group. Of the 280 species in the Megascolecidae *sensu* Gates, some 130 are from the Indian region, 130 from Australia and the residue from New Zealand. As previously mentioned, the *Pheretima* group originated on the Australian Plate so its closest allies might be expected to be present among the indigenous Megacolecidae of Australia.

Taxonomy

The component species of the *Pheretima* group of genera are readily distinguishable from the members of the other genera forming the family Megascolecidae (sensu Gates, 1959) by the presence of an oesophageal gizzard in segment *viii.* The gizzard is usually well developed to the extent that it often lies within the parietes of not only segment *viii* but also segments *ix* and *x*. In *Pleionogaster*, however, the oesophageal gizzard is only vestigial and here it is replaced functionally by intestinal gizzards which are diagnostic of the genus. Additionally all pheretimoids are perichaetine.

The species of this group of genera form two loose assemblages; those with a pair of lateral caeca or a single median caecum arising from the anterior region of the intestine, and those without this specialization. The latter category, the 'acaecate' species are revised here and assigned to five genera: *Archipheretima*, *Metapheretima* (inc. *Ephmitra*), *Planapheretima*, *Pleionogaster* and *Polypheretima.* On the basis of the numerical investigations described above and detailed under the genera concerned, the species are often placed in divisions and species-groups also, in two instances, species-complexes are recognized. Some of these infra-generic categories may represent superspecies while others may, in time, be considered to represent subgenera, but until further information becomes available, they should be regarded as being no more than aggregations of morphologically similar species placed together to facilitate identification. They are not coordinate, even within any one genus. One of the species-complexes recognized was erected to contain five closely allied taxa comprising the *Polypheretima elongata* species-complex (Easton, 1976). At the present time the mutual relationships of these taxa are unknown, in many ways the complex resembles a polytypic species.

The majority of acaecate species are known from only one or two series, and whenever possible examples of all known records have been examined in this study. The following abbreviations have been utilized to denote the institution in which material is deposited.

Adelaide	South Australian Museum
Amsterdam	Zöologisch Museum, Universitat van Amsterdam
Berlin	Museum für Naturkunde an der Humbolt-Universität zu Berlin
Bogor	Museum Zoologicum Bogoriense, Bogor, Indonesia
BMNH	British Museum (Natural History)
Cambridge	University Museum of Zoology, Cambridge, England
Genoa	Museo Civico di Storia Naturale 'Giacomo Doria'

Hamburg	Zoologisches Institut und Zoologisches Museum, Universität Hamburg
Honolulu	Bernice P. Bishop Museum
Leiden	Rijksmuseum van Natuurlijke Historie
New York	American Museum of Natural History
Stockholm	Naturhistoriska Riksmuseet
Turin	Museo ed Instituto di Zoologica Systematica, Università di Turin
Vienna	Naturhistorisches Museum Wein

Aclitellate and clitellate individuals among the material examined are indicated by the letters A and C respectively.

Key to the genera of the *Pheretima* group

1	Setae crowded ventrally, creeping sole present, body usually flattened dorsoventrally	***Planapheretima*** (p. 64)
	Setae not crowded ventrally, creeping sole absent, body always cylindrical	2
2	Intestine lacking caecum(a) or gizzards	3
	Intestine with gizzards	***Pleionogaster*** (p. 114)
	Intestine with caecum(a)	5
3	Crescentic markings associated with male pores (Fig. 4c)	***Metapheretima*** (p. 78)
	Crescentic markings absent	4
4	Clitellum extending over more than three segments; spermathecal diverticula multilocular	***Archipheretima*** (p. 21)
	Clitellum restricted to three segments, spermathecal diverticula simple	***Polypheretima*** (p. 28)
5(2)	Intestinal caecum(a) originating in or near segment *xxii*	***Pithemera***[1]
	Intestinal caecum(a) originating in or near segment *xxvii*	6
6	Male pores simple	***Amynthas***[1]
	Male pores within copulatory pouches	7
7	Nephridia on spermathecal ducts	***Pheretima***[1]
	Nephridia absent from spermathecal ducts	***Metaphire***[1]

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[1] For keys to the nominal species and species-groups of the 'caecate' genera, *Amynthas*, *Metaphire*, *Pheretima* and *Pithemera*, see Sims & Easton (1972). For species transferred to these genera since 1972 see below (p. 119).

ARCHIPHERETIMA Michaelsen, 1928

Megascolex (part): Beddard, 1895 : 370.
Amynthas (part): Beddard, 1900*a* : 612.
Pheretima (part): Michaelsen, 1900 : 234.
Pheretima (*Archipheretima*) (part) Michaelsen, 1928*a* : 7.
Pheretima (*Archipheretima*): Michaelsen, 1934*b* : 15.
Archipheretima: Sims & Easton, 1972 : 200, 232.

TYPE SPECIES. *Megascolex iris* Michaelsen, 1892, original designation.

DIAGNOSIS. Megascolecidae with an oesophageal gizzard in *viii*, intestinal caeca and gizzards absent. Body cylindrical, setae never excessively crowded ventrally, creeping sole absent. Male pores superficial or on circular porophores, never within copulatory pouches. Spermathecal diverticula multilocular.

DESCRIPTION. Body cylindrical. Clitellum annular, extending over four or more segments in mature individuals (*xii*, *xiii–xvi*, *xvii*, *xviii*). Dorsal pores present from 12/13. Setae perichaetine with large dorsal gaps (up to 0·25 body circumference), often slightly crowded ventrally. Lateral hearts in *x–xii* and sometimes *xiii*.

Oesophagus with a well-developed gizzard in *viii*, lacking dorsal pouches and calciferous glands. Intestine begins between *xv* and *xvii*, simple, lacking caeca, gizzards and glandular walls.

Holandric, testes free (?) or in large, delicate sacs lining the coelom and usually enclosing the anterior seminal vesicles, the lateral hearts and other vessels. Seminal vesicles paired in *xi* and *xii*.

Prostates racemose. Paired, combined male and prostatic pores on the ventral surface of *xviii* in the setal ring. Male pores occasionally on porophores which may be elongate and extend onto *xix* and *xx*. Copulatory pouches absent. Ovaries free. Oviducts leading to single or closely paired midventral equatorial pore(s) on *xiv*. Spermathecae only slightly differentiated into duct and ampulla; each with a short multilocular diverticulum. Spermathecae arranged in pairs in three or four adjacent segments between *v* and *ix*. Spermathecal pores always intersegmental, small, often slitlike, ventral or ventrolateral.

Genital markings of two kinds have been recorded; discrete paired, ovoid segmental markings and diffuse intersegmental markings. The porophores extending from *xviii* to *xx* in some species may be confused with genital markings.

DISTRIBUTION. Borneo, Philippines.

INCLUDED SPECIES. *iris* species-group (*iris*, *margaritacea*, *mazarredi*, *zonata*), *ophiodes*, *picta*.

NUMERICAL STUDIES. In the initial computer study (see above) the affinities of the species as revealed by the MST and their configuration on the first and second vectors (Fig. 6) provide the basis for the recognition of two distinct species and one species-group.

REMARKS. Although a key is provided for the identification of species included in the genus *Archipheretima*, mature individuals may be readily assigned to their species or species-group on the form of their genital markings (Figs 11 and 12). The species *tumifaciens* (Lee, 1967) which was provisionally included in *Archipheretima* by Sims & Easton (1972) is now transferred to *Metapheretima* as a synonym of *M. jocchana* (Cognetti, 1911).

Key to the species of the genus *Archipheretima*

1	First spermathecal pores in furrow 4/5 (3 thecal segments)	***ophiodes*** (p. 27)
	First spermathecal pores in furrow 5/6 (4 thecal segments)	2
	First spermathecal pores in furrow 6/7 (3 thecal segments)	4
2	Spermathecal pores closely paired (0·05 body circumference apart) . . .	***zonata*** (p. 23)
	Spermathecal pores widely paired (0·20–0·30 body circumference apart)	3
3	Male pore small, indistinct (Philippines)	***mazarredi*** (p. 23)
	Male pore at centre of large porophore (Borneo)	***picta*** (p. 26)
4(1)	Spermathecal pores *c.* 0·05 body circumference apart (preclitellar genital markings absent)	***iris*** (p. 26)
	Spermathecal pores *c.* 0·10 body circumference apart (preclitellar genital markings present)	***margaritacea*** (p. 25)

Archipheretima iris species-group

DIAGNOSIS. *Archipheretima* with poorly defined intersegmental genital markings and simple male pores.

DISTRIBUTION. Borneo and Philippines.

SPECIES INCLUDED. *iris*, *margaritacea*, *mazarredi*, *zonata*.

REMARKS. Juvenile and other individuals with poorly developed genital markings may be distinguished from *picta* by the absence of a porophore and from *ophiodes* by the presence of spermathecal pores in furrow 7/8. Marker characters of the species included in the *iris* species-group are given in Table 4.

Archipheretima mazarredi (Rosa, 1894)

Megascolex mazarredi Rosa, 1894 : 6.
Amynthas mazarredoi: Michaelsen, 1899 : 15; Beddard, 1900*a* : 644.
Pheretima mazarredoi: Michaelsen, 1900 : 283; Gates, 1970*a* : 155.
Archipheretima mazarredoi: Sims & Easton, 1972 : 232.

DIAGNOSIS. *Archipheretima* with spermathecal pores about one fifth of the body circumference apart in furrows 5/6/7/8/9. Genital markings poorly defined, intersegmental.

DESCRIPTION. *External characters.* Length 200–325 mm, diameter 13–15 mm. 105–131 segments. Clitellum *xiii–xvi*. First dorsal pore 12/13. Setae *c.* 100 on *xxv*, setal ring crowded ventrally.

Table 4 Marker characters of the members of the *Archipheretima iris* species-group

Species	Spermathecal furrows	Separation of spermathecal pores	Setal No. on *vii*	Genital markings	Distribution
mazarredi	5/6/7/8/9	0·20	*c.* 100	postclitellar	Marinduque Is. Philippines
zonata	5/6/7/8/9	0·05	*c.* 94	postclitellar	Borneo
margaritacea	6/7/8/9	0·10	*c.* 28	preclitellar and postclitellar	Samar Is. Philippines
iris	6/7/8/9	0·05	34–40	postclitellar	Samar Is. Philippines

Male pores *c.* 0·20 body circumference apart. Female pore single. Spermathecal pores paired, 5/6/7/8/9, *c.* 0·20 body circumference apart.

Genital markings (Fig. 11a) diffuse, paired, intersegmental in line with the male pores in 17/18 and 18/19, 19/20, 20/21.

Internal characters. Septa anterior to 17/18 thickened. Intestine begins in *xvii*. Lateral hearts in *x–xiii*.

Holandric, testes in *x* and *xi*, testes sacs membranous or absent, seminal vesicles in *xi* and *xii*. Spermathecae (Fig. 10a) paired in *vi–ix*.

Description after Rosa (1894) and Gates (1970). Fig. 11a is an interpretation of the genital field based on the written descriptions.

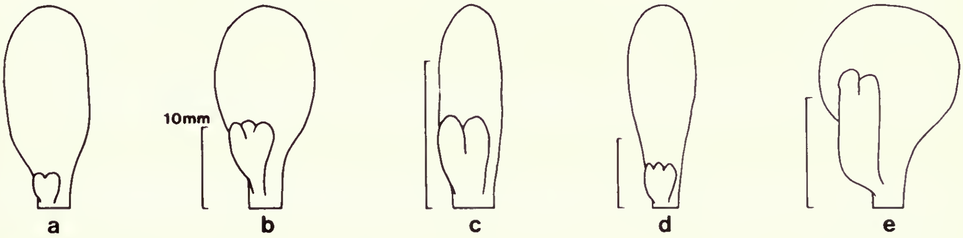

Fig. 10 Spermathecae. (a) *Archipheretima mazarredi*; (b) *A. zonata*; (c) *A. margaritacea*; (d) *A. iris*; (e) *A. picta*. Scales 1 mm unless otherwise indicated.

Distribution. Marinduque Island, Philippines.

Remarks. The correct spelling of the name *mazarredi* has been the subject of confusion. The original orthography, *mazarredi*, was changed by Michaelsen (1900) to *mazarredoi*, an unjustified emendation (Article 33, *Int. Code zool. Nomencl.*) which has been used by subsequent authors.

Records. 1C Marinduque Island, Philippines (holotype of *mazarredi*). It has not been possible to locate the holotype of this species. It is absent from the collection of the Museo Nacional de Ciencias Naturales, Madrid, where Gates (1970) suggested that it may be found: Dr J. Alvarez, personal communication. 7A Marinduque Island, Philippines (*mazarredi*: Gates, 1970).

Archipheretima zonata (Michaelsen, 1922)

Pheretima zonata Michaelsen, 1922 : 42.
Pheretima (*Archipheretima*) *zonata*: Michaelsen, 1928*a* : 11; Michaelsen, 1934*b* : 15.
Archipheretima zonata: Sims & Easton, 1972 : 181, 232.

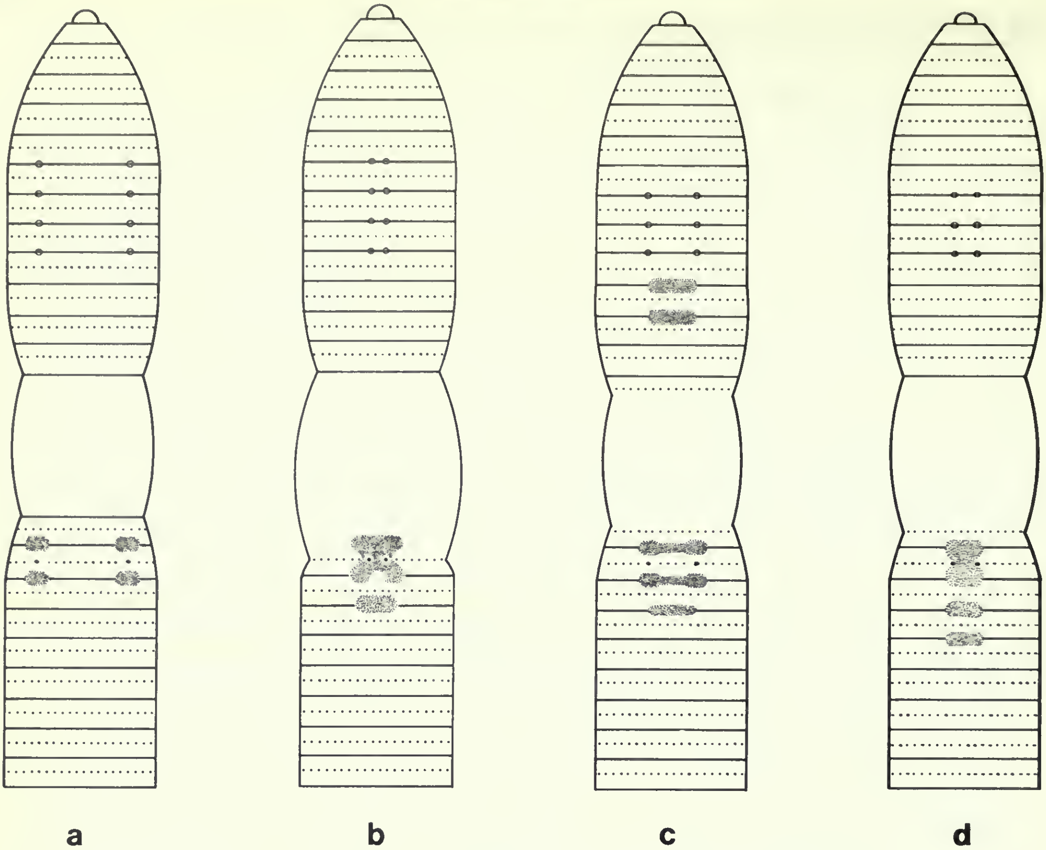

Fig. 11 Anterior ventral surface, diagnostic characters. (a) *Archipheretima mazarredi*; (b) *A. zonata*; (c) *A. margaritacea*; (d) *A. iris*.

Pheretima (*Archipheretima*) *penrisseni* Michaelsen, 1928*a* : 11; Michaelsen, 1934*b* : 15.
Archipheretina penrisseni: Sims & Easton, 1972 : 232.

DIAGNOSIS. *Archipheretima* with spermathecal pores about one twentieth of the body circumference apart in furrows 5/6/7/8/9. Genital markings poorly defined, intersegmental.

DESCRIPTION. *External characters*. Length 190–360 mm, diameter 10–15 mm. 124–147 segments. Clitellum ½*xiii*–½*xviii*. First dorsal pore 12/13. Setae 90–94 on *vii*, 84–96 on *xx*. Setal ring slightly crowded ventrally on preclitellar segments ($aa = ab = 0{\cdot}6yz = 0{\cdot}6zz$), and with dorsal gaps on postclitellar segments ($aa = ab = 0{\cdot}6yz = 0{\cdot}3zz$).

Male pores simple, *c*. 0·05 body circumference apart. Female pore single or paired. Spermathecal pores small, paired, 5/6/7/8/9, *c*. 0·04 body circumference apart.

Genital markings (Fig. 11b), single or paired, intersegmental in 17/18, 18/19, 19/20.

Internal characters. Septa 5/6–7/8 thickened, 8/9 membranous, 9/10–13/14 thickened. Intestine begins in *xvi*. Lateral hearts in *x*–*xii*.

Holandric, testes sacs annular, enclosing the lateral hearts, in *x* and, in *xi* the anterior seminal vesicles as well. Spermathecae (Fig. 10b) paired in *vi*–*ix*.

DISTRIBUTION. Borneo.

REMARKS. Genital markings are absent from the holotype of *zonata* while the clitellum has not developed to its full length in the holotype of *penrisseni*. These differences are probably attributable to differential rates of achieving maturity.

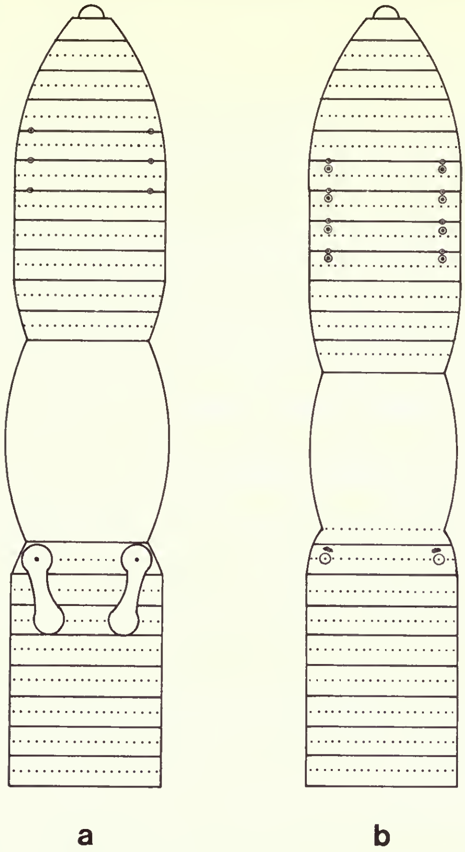

Fig. 12 Anterior ventral surface, diagnostic characters. (a) *Archipheretima ophiodies;* (b) *A. picta.*

Material examined. 1C Nangaraun, Kalimanton; Leiden 1816 (holotype of *zonata*). 1C Mt Penrissen, Sarawak; Hamburg v10513 (holotype of *penrisseni*).

Archipheretima margaritacea (Michaelsen, 1892)

Megascolex margaritacea Michaelsen, 1892 : 245; Beddard, 1895 : 383.
Amynthas margaritacea: Michaelsen, 1899 : 16; Beddard, 1900*a* : 647.
Pheretima margaritacea: Michaelsen, 1900 : 282.
Pheretima (*Archipheretima*) *margaritacea*: Michaelsen, 1934*b* : 15.
Archipheretima margaritacea: Sims & Easton, 1972 : 232.

Diagnosis. *Archipheretima* with spermathecal pores about one tenth of the body circumference apart in furrows 6/7/8/9. Genital markings poorly defined, intersegmental in furrows 9/10, 10/11, 12/13 and in postclitellar furrows.

Description. *External characters*. Length *c*. 90 mm, diameter *c*. 5 mm. 85–103 segments. Clitellum ¼*xiii*–¼*xvii*. First dorsal pore 12/13. Setae, *c*. 28 on *vii*, *c*. 28 on *xx*, setal ring regular on preclitellar segments with dorsal and ventral gaps ($aa=2ab=2yz=0{\cdot}5zz$), slightly crowded ventrally with dorsal and ventral gaps on postclitellar segments ($aa=2ab=yz=0{\cdot}5zz$).

Male pores simple, *c*. 0·10 body circumference apart. Female pores paired. Spermathecal pores small transverse slits, 6/7/8/9, *c*. 0·10 body circumference apart.

Genital markings (Fig. 11c), diffuse, unpaired, median, intersegmental in 10/11, 17/18, 18/19, 19/20 and occasionally 9/10 and 12/13.

Internal characters. Not known. Spermathecae (Fig. 10c) paired in *vii–ix*.

DISTRIBUTION. Samar Island, Philippines.

REMARKS. Michaelsen (1892) did not describe the internal morphology of this species. All the internal structures in the anterior region except the spermathecae have been removed from the surviving syntype by previous dissection. It is probable that the internal anatomy of this species resembles that of *iris*.

MATERIAL EXAMINED. 1A (lacking anterior portions of gut and anterior male reproductive organs) Loquilocon, Samar Island, Philippines; Hamburg v361 (syntype of *margaritacea*).

OTHER MATERIAL. Data as above; Berlin 2134 (syntype(s) of *margaritacea*). This material could not be located during the preparation of this report: Dr G. Hartwich, personal communication.

Archipheretima iris (Michaelsen, 1892)

Megascolex iris Michaelsen, 1892 : 244; Beddard, 1895 : 383.
Amynthas iris: Michaelsen, 1899 : 15; Beddard, 1900*a* : 647.
Pheretima iris: Michaelsen, 1900 : 276.
Pheretima (*Archipheretima*) *iris*: Michaelsen, 1928*a* : 8; Michaelsen, 1934*b* : 15.
Archipheretima iris: Sims & Easton, 1972 : 200, 232.

DIAGNOSIS. *Archipheretima* with spermathecal pores about one twentieth of the body circumference apart in furrows 6/7/8/9. Genital markings poorly defined, intersegmental in postclitellar furrows only.

DESCRIPTION. *External characters.* Length 170–240 mm, diameter 7–9 mm. 110–116 segments. Clitellum *xiii*–½*xvii*. First dorsal pore 12/13. Setae, 34–40 on *vii*, 42–46 on *xx*, setal ring slightly crowded ventrally with dorsal and ventral gaps ($aa = 2ab = yz = 0{\cdot}25zz$).

Male pores simple, *c.* 0·05 body circumference apart. Female pore single. Spermathecal pores paired, small transverse slits, 6/7/8/9, *c.* 0·05 body circumference apart.

Genital markings (Fig. 11d) diffuse unpaired, median, intersegmental in 17/18, 18/19, 19/20, 20/21.

Internal characters. Septa 6/7–12/13 membranous. Intestine begins in *xvii*. Lateral hearts in *x–xiii*.

Holandric, testes sacs large, annular in *x* and *xi*, enclosing the lateral hearts and in *xi* the seminal vesicles as well, seminal vesicles small, extending to the lateral line. Spermathecae (Fig. 10d) paired *vii–ix*.

DISTRIBUTION. Samar Island, Philippines.

REMARKS. The description differs in some details from those of earlier authors (Michaelsen, 1892; Sims & Easton, 1972). Michaelsen recorded the number of segments in this species as 240, neither of the clitellate specimens examined had more than 116 segments, but both approached the maximum length of 240 mm recorded by Michaelsen. Sims and Easton recorded the separation of the male and spermathecal pores as 0·25 but an examination of the type series confirmed that the value should be 0·05 as contained in the original description.

MATERIAL EXAMINED. 2C, 2A Loquilocon, Samar Island, Philippines; Berlin 565 (syntypes of *iris*). 1A Data as above; Turin 01 122 (syntype of *iris*).

Archipheretima picta (Michaelsen, 1892)

Megascolex pictus Michaelsen, 1892 : 246; Beddard, 1895 : 384.
Amynthas pictus: Michaelsen, 1899 : 83; Beddard, 1900*a* : 623.
Pheretima picta: Michaelsen, 1900 : 294.
Pheretima (*Archipheretima*) *picta*: Michaelsen, 1928*a* : 10; Michaelsen, 1934*b* : 15.
Archipheretima picta: Sims & Easton, 1972 : 230.

Pheretima beccarii Cognetti, 1909 : 331.
Pheretima (*Archipheretima*) *beccarii*: Michaelsen, 1928*a* : 11.
Archipheretima beccarii: Sims & Easton, 1972 : 230.

DIAGNOSIS. *Archipheretima* with spermathecal pores about one quarter of the body circumference apart in furrows 5/6/7/8/9. Male pores on circular porophores. Genital markings ovoid, paired, presetal on *vi–ix* and *xviii*.

DESCRIPTION. *External characters.* Length 240–260 mm, diameter, 5–9 mm. 137–146 segments. Clitellum *xiii*–¼*xviii*. First dorsal pore 12/13. Setae, *c.* 74 on *vii*, *c.* 77 on *xx*, setal ring regular with dorsal gaps on preclitellar segments ($aa=ab=yz=0{\cdot}3zz$), slightly crowded ventrally with dorsal and ventral gaps on postclitellar segments ($aa=2ab=yz=0{\cdot}3zz$).

Male pores on circular porophores *c.* 0·29 body circumference apart. Female pore single. Spermathecal pores small in 5/6/7/8/9 *c.* 0·27 body circumference apart.

Genital markings (Fig. 12b) paired, presetal, in line with the spermathecal pores, on *vi–ix*, anterior to the male pores on *xviii*.

Internal characters. Septa 5/6/7/8 slightly thickened, 8/9 absent, 9/10–13/14 slightly thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs annular in *x* and *xi*, seminal vesicles large, extending to the dorsal line in *xi* and *xii*, those of *xi* enclosed in the posterior testes sacs. Spermathecae (Fig. 10e) paired in *vi–xi*.

DISTRIBUTION. Borneo.

REMARKS. The original description of *picta* did not contain details of the genital markings or mention of intestinal caeca. Later Michaelsen (1900 : 248) was uncertain whether *picta* possessed intestinal caeca, although finally he included it in the subgenus *Archipheretima* (1928 : 10). In the absence of typical material, it is proposed to accept Michaelsen's decision since the other characters he listed, length of clitellum and form of spermathecal diverticula, support the inclusion of the species in *Archipheretima*.

The holotype of *beccarii* agrees closely with the description of *picta*, being distinguishable only by a shorter clitellum and the presence of genital markings. These differences are probably attributable to varying stages of development.

MATERIAL EXAMINED. 1C Sarawak; Genova 44045 (holotype of *beccarii*).

OTHER RECORDS. 1C Sampit, Kalimanton; Berlin 554 (holotype of *picta*). This specimen is listed in the catalogue of the Berlin Museum but it could not be located during the preparation of this paper: Dr G. Hartwich, personal communication.

Archipheretima ophiodes (Michaelsen, 1929)

Pheretima (*Archipheretima*) *ophiodes* Michaelsen, 1929 : 85; Michaelsen, 1930*a* : 273; Michaelsen, 1934*b* : 15.
Archipheretima ophiodes: Sims & Easton, 1972 : 230.

DIAGNOSIS. *Archipheretima* with spermathecal pores in furrows 4/5/6/7. Male pores on raised porophores extending from *xviii* to *xx*.

DESCRIPTION. *External characters.* Length 245–300 mm, diameter 13–20 mm. 106–118 segments. Clitellum *xii–xvii*. First dorsal pore 12/13. Setae, *c.* 60 on *vii*, *c.* 67 on *xxvi*, *c.* 72 on *xxx*, setal ring crowded ventrally with very large dorsal gaps ($zz=0{\cdot}25$ body circumference).

Male pores simple, on raised porophores extending from *xviii* to *xx* (Fig. 12a), separation not recorded. Female pores paired. Spermathecal pores in 4/5/6/7, *c.* 0·33 body circumference apart.

Genital markings absent.

Internal characters. All anterior septa present and delicate. Beginning of intestine not recorded. Lateral hearts in *x–xiii*.

Holandric, testes sacs in *x* and *xi*, details not recorded. Seminal vesicles in *xi* and *xii*, simple, thin. Spermathecae paired in *v–vii*, ampulla sack-like or pear-shaped, not differentiated into ampulla and duct, diverticula small, globular.

Description after Michaelsen (1929, 1930); and the author after the examination of the remains of a syntype.

DISTRIBUTION. Luzon, Philippines.

MATERIAL EXAMINED. The gizzard, oesophagus, part of the intestine and part of the anterior male reproductive system (the body wall has not survived). Mt Azapan, Luzon, Philippines; Hamburg v10418 (remains of syntype of *ophiodes*).

POLYPHERETIMA Michaelsen, 1934

Megascolex (*Perriera*) (part) Vaillant, 1889 : 63.
Perichaeta (part): Beddard, 1895 : 388.
Amynthas (part): Beddard, 1900*a* : 612.
Pheretima (part): Michaelsen, 1900 : 234.
Pheretima (*Parapheretima*) (part) Cognetti, 1912 : 556; Michaelsen, 1928*a* : 8.
Pheretima (*Pheretima*) (part): Michaelsen, 1928*a* : 8.
Pheretima (*Metapheretima*) (part): Michaelsen, 1928*a* : 8.
Metapheretima (part): Sims & Easton, 1972 : 205, 233.
Pheretima (*Polypheretima*) (part) Michaelsen, 1934*b* : 15.

TYPE SPECIES. *Perichaeta stelleri* Michaelsen, 1892, original designation.

DIAGNOSIS. Megascolecidae with an oesophageal gizzard in *viii*, intestinal caeca and gizzards absent. Body cylindrical, setae never excessively crowded ventrally, creeping sole absent. Male pores on circular porophores which may be within copulatory pouches. Crescentic genital markings absent. Spermathecal pores small, spermathecal diverticula simple and usually ectal in origin.

DESCRIPTION. Body cylindrical, creeping sole absent. Clitellum annular, restricted to three segments (*xiv–xvi*). First dorsal pore between 5/6 and 12/13. Setae perichaetine, never excessively crowded ventrally, dorsal and ventral gaps small ($aa=1\text{–}2ab$, $zz=1\text{–}2yz$). Lateral hearts in *x–xii* and sometimes *xiii*.

Oesophagus with a well-developed gizzard in *viii* but lacking calciferous glands and dorsal pouches. Intestine begins in *xv* or *xvi*, simple, lacking caeca, gizzards and glandular walls.

Usually holandric, occasionally metandric, ? never proandric – testes may be restricted to *x* in *sibogae* which is known only from the damaged holotype. The testes of each segment are enclosed in single or paired stout sacs which usually occupy most of the coelom and often enclose the anterior seminal vesicles and the lateral hearts of *x* and *xi*. One pair of seminal vesicles in the segment directly posterior to each pair of testes. Prostates racemose. Paired combined male and prostatic pores on the ventral surface of *xviii* in the setal ring. Male pores situated on circular porophores, often within copulatory pouches. The porophores bearing the male pores are short and stout (cf. penial bodies in *Metapheretima*) while the openings to the copulatory pouches, when present, are often crescentic (Figs 3a–f). Ovaries free in *xiii*. Oviducts lead to single or closely paired, midventral, equatorial pore(s) on *xiv*. Spermathecae each differentiated into duct and ampulla, diverticula simple and ectal in origin, usually as long or longer than main duct and ampulla. Spermathecae arranged in pairs or paired batteries of up to 28 spermathecae, in one to five adjacent segments between *v* and *ix*. Spermathecal pores small, usually intersegmental, rarely segmental.

Genital markings always of the discrete type, diffuse genital markings and annular ridges absent. When present on *xviii* the genital markings are identical to those of adjacent segments; they are never crescentic and closely associated with the male pores. The arrangement of genital markings is variable. The glandular tissue associated with the genital markings may be restricted to the body wall or invade the coelom in the form of stalked glands. The area around the male pores may be infrequently elevated above the body surface.

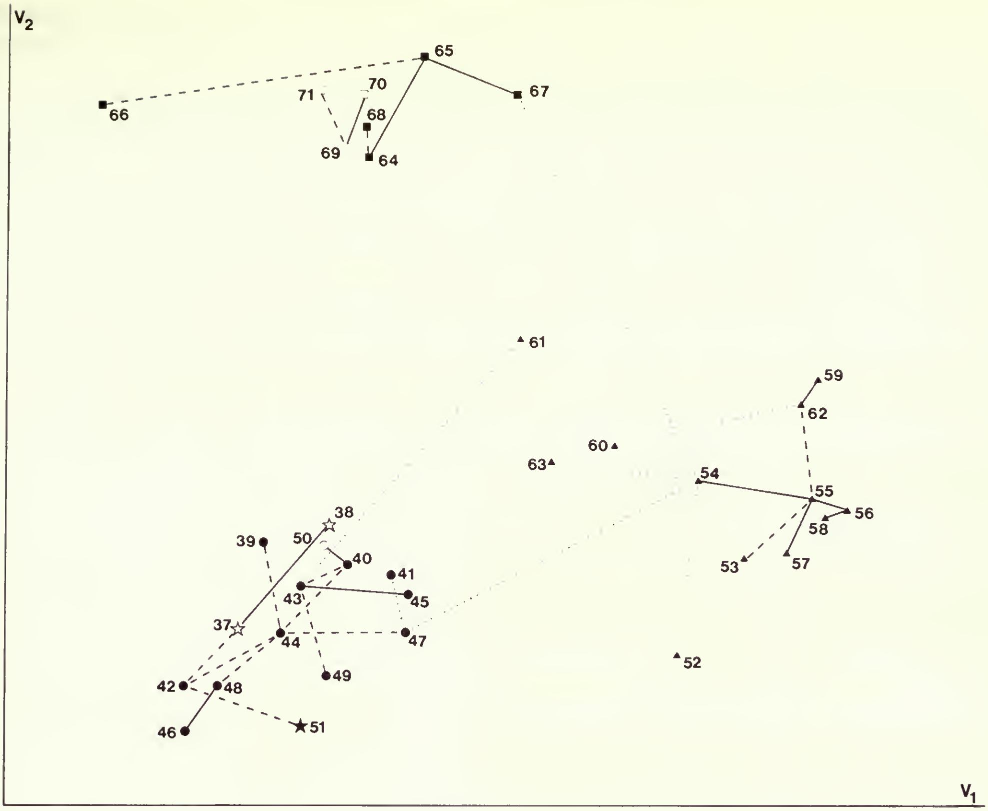

Fig. 13 Principal co-ordinates analysis of 35 species here assigned to *Polypheretima* (37–71 of Table 1): the configuration of species with the vectors corresponding to the first and second latent roots. The linkages of the added MST are graded to indicate percentage similarities; ——, +95%; - - - - -, 90–95%; · · · · ·, −90%. Three major assemblages are recognized:

Division I – circular and star-shaped symbols (closed circles – *bifaria* species-group, open circle – *grata*, closed stars – *annulata* species-complex, open star – *voeltzkowi*).

Division II – triangular symbols (*polytheca* species-group).

Division III – square symbols (closed squares – *badia* species-group, open squares – *patae* species-group).

Distribution. (Fig. 8.) Autochthonous species have been recorded throughout the *Pheretima* group domain except from New Britain, the Solomon Islands, New Hebrides, Caroline Islands and Marianas.

Numerical studies. The taxa of the genus *Polypheretima* listed in Table 1 (37–71) were subjected to a numerical analysis utilizing the characters listed in Table 2. The configuration of the taxa with the first and second vectors of the principal co-ordinates analysis as axes, to which the MST with graded linkages has been added, is shown in Fig. 13. Three divisions, indicated by circular, triangular and square symbols, may be recognized. The division to which the species *pentacystis* (61) should be assigned requires discussion. From its position on the first and second vectors it would appear to belong to Division II (triangular symbols), although it is linked by the MST to Division I (circular symbols). Since this species possesses several characters diagnostic of Division II as well as having several nearest neighbours among the taxa of this division, it is proposed to include *pentacystis* in Division II.

Morphologically the three divisions are readily defined. All holandric taxa are accommodated in Divisions I and II while metandric species form Division III (square symbols). With the exception of the species *grata* (50) all the members of Division I have simple male pores while those of

Division II have male pores within copulatory pouches. The copulatory pouches of *grata* differ from those of members of Division II in that stalked glands discharge into them in addition to the male pores.

An examination of all of the vectors available for study failed to reveal the presence of subordinate clusters within Division I. Nevertheless it is convenient to recognize a species group, a species-complex and two species within this division. The individual species are *grata* (50) discussed above and *voeltzkowi* (51) with postsetal spermathecal pores. The members of the *annulata* species complex, *annulata* (37) and *fakfakensis* (38), have presetal spermathecal pores. The *bifaria* species-group is recognized by the possession of simple male pores and intersegmental spermathecal pores.

All of the taxa in Division II are assigned to the *polytheca* species-group. Included in this species-group are taxa 54–58 the *elongata* species-complex which are linked by the MST at very high levels.

Table 5 Phenetic classification and checklist of the genus *Polypheretima*

Division I		*annulata* species-complex	*annulata* (37)
			fakfakensis (38)
	bifaria species- group	*bifaria* (39)	
		brevis (40)	
		fida (41)	
		gatesi (42)	
		iizukai (43)	
		mertoni (44)	
		moelleri	
		monticola (45)	
		panarana (46)	
		sempolensis (47)	
		sepikensis (48)	
		taprobaenae (49)	
		grata (50)	
		voeltzkowi (51)	
Division II	*polytheca* species-group	*annamensis* (52)	
		aringeana (53)	
		elongata species-complex	*elongata* (54)
			everetti (55)
			kinabaluensis (56)
			phacellotheca (57)
			stelleri (58)
		koyana (59)	
		lesonea (60)	
		pentacystis (61)	
		polytheca (62)	
		renschi (63)	
Division III	*badia* species-group	*badia* (64)	
		elberti (65)	
		kellneri (66)	
		sibogae (68)	
		swelaensis (67)	
	patae species-group	*coplandi* (69)	
		huonensis	
		kershawae (70)	
		patae (71)	

Numbers in parentheses indicate taxa assessed in numerical studies (see Figs 6 and 13).

The taxa forming Division III can be readily divided into two clusters, indicated by open and closed square symbols, on the position of the species along the third vector (not shown here) and by application of the MST. The cluster indicated by solid square symbols, the *badia* species-group, comprises taxa from the Lesser Sunda Islands, these have a single pair of genital markings on each of several postclitellar segments. While the clusters indicated by open square symbols, the *patae* species-group, contains taxa from New Guinea with numerous genital markings arranged in transverse rows on several postclitellar segments.

A summary of the phenetic classification based on this numerical investigation is given in Table 5.

Key to the species of the genus *Polypheretima*

1	Proandric	***sibogae***[1] (p. 58)
	Holandric	2
	Metandric	21
2	Male pores simple	3
	Male pores in copulatory pouches	13
3	Spermathecal pores segmental	4
	Spermathecal pores intersegmental	5
4	Spermathecal pores presetal (*vii*, *viii* or *vii*, *viii*, *ix*)[2]	***annulata*** species-complex (p. 34)
	Spermathecal pores postsetal (*v* only)	***voeltzkowi*** (p. 47)
5(3)	First spermathecal pores in furrow 4/5	6
	First spermathecal pores in furrow 5/6	7
	First spermathecal pores in furrow 6/7	12
	First spermathecal pores in furrow 7/8 (one thecal segment)[3]	***taprobanae*** (p. 45)
6	Two or three thecal segments[4]	***fida*** (p. 37)
	Five thecal segments	***moelleri*** (p. 38)
7(5)	Two thecal segments	8
	Three thecal segments	10
	Four thecal segments[5]	11
8	One pair of genital markings per segment (Java)	***sempolensis*** (p. 39)
	Two or more pairs of genital markings per segment (New Guinea area)	9
9	Glands to genital markings confined to body wall	***mertoni*** (p. 40)
	Glands to genital markings stalked, occupy coelom	***sepikensis*** (p. 40)
10(7)	Bithecal[6]	***brevis*** (p. 41)
	Polythecal	***bifaria*** (part) (p. 41)
11(7)	Genital markings presetal only (Philippines)	***monticola*** (p. 42)
	Genital markings pre- and postsetal (New Guinea)	***bifaria*** (part) (p. 41)
	Genital markings postsetal only (Japan)	***iizukai*** (p. 43)
12(5)	Spermathecal pores *c.* 0·3 body circumference apart (genital markings as fig. 20b)	***panarana*** (p. 45)
	Spermathecal pores *c.* 0·5 body circumference apart (genital markings as fig. 20a)	***gatesi*** (p. 44)
13	First spermathecal pores in furrow 4/5 (five thecal segments)	***pentacystis*** (p. 48)
	First spermathecal pores in furrow 5/6	14
	First spermathecal pores in furrow 6/7	19
	First spermathecal pores in furrow 7/8 (two thecal segments)	***renschi*** (p. 56)
14	One or two thecal segments	15
	Four thecal segments	17
15	Stalked glands discharge into copulatory pouches; external postclitellar genital markings absent	***grata*** (p. 46)
	Copulatory pouches lack stalked glands; external postclitellar genital markings present.	16
16	Postclitellar genital markings simple, presetal; spermathecal pores *c.* 0·25 body circumference apart	***elongata*** species-complex (part) (p. 52)
	Postclitellar genital markings complex, occupying whole length of segment; spermathecal pores *c.* 0·50 body circumference apart	***aringeana*** (p. 55)
17(14)	Spermathecal batteries with 6–10 spermathecae in each (Malaya and Borneo)	18
	Spermathecal batteries with 1 spermatheca in 5/6/7/8, 8–10 in 8/9 (Sumatra)	***lesonea*** (part) (p. 51)

18 Male pores *c.* 0·17 body circumference apart (Borneo) . . . . . ***koyana*** (p. 50)
Male pores *c.* 0·24 body circumference apart (Malaya) . . . . ***polytheca*** (p. 49)
19(13) One thecal segment 20
Three thecal segments . . . . ***lesonea*** (part) (p. 51)
20 Spermathecal batteries with 1 spermatheca in each (Vietnam) . . ***annamensis*** (p. 56)
Spermathecal batteries with more than 1 spermatheca in each (Indonesia)
elongata species-complex (part) (p. 52)
21(1) Papuan specimens 22
Specimens from the Lesser Sunda Islands 23
22 Two thecal segments (*vi–vii*); spermathecal pores *c.* 0·33 body circumference apart
huonensis (p. 63)
Three thecal segments (*v–vii*); spermathecal pores *c.* 0·42 body circumference apart
coplandi (p. 62)
Four thecal segments (*v–viii*); spermathecal pores *c.* 0·26 body circumference apart
kershawae (p. 62)
Five thecal segments (*v–ix*); spermathecal pores *c.* 0·55 body circumference apart
patae (p. 61)
23(21) First spermathecal pores in furrow 4/5 24
First spermathecal pores in furrow 5/6[7] 26

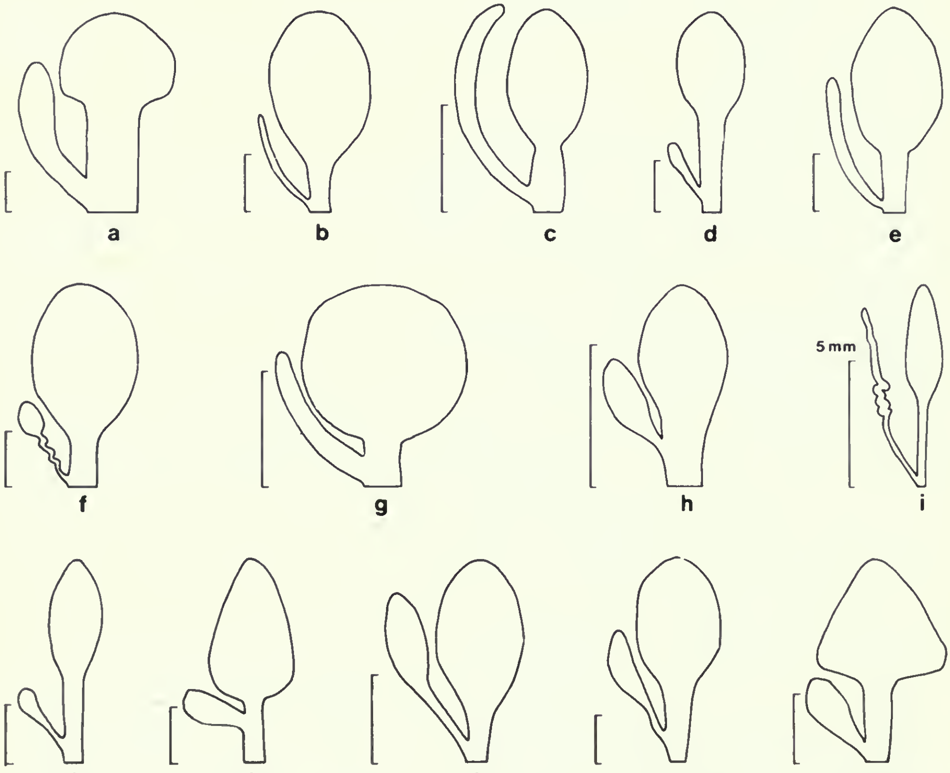

Fig. 14 Spermathecae. (a) *Polypheretima annulata*; (b) *P. fida*; (c) *P. moelleri*; (d) *P. sempolensis* sp. nov.; (e) *P. mertoni*; (f) *P. sepikensis*; (g) *P. brevis*; (h) *P. bifaria*; (i) *P. izzukai*; (j) *P. gatesi* sp. nov.; (k) *P. panarana*; (l) *P. taprobanae*; (m) *P. grata*; (n) *P. veoltzkowi*. All scales 0·5 mm unless otherwise indicated.

24	Bithecal	25
	Polythecal	***sibogae***[1] (p. 58)
25	Spermathecal pores *c.* 0·3 body circumference apart	***badia*** (part) (p. 59)
	Spermathecal pores *c.* 0·5 body circumference apart	***kellneri*** (p. 57)
26(23)	Three thecal segments	***swelaensis*** (p. 60)
	Four thecal segments	27
27	Spermathecal pores *c.* 0·3 body circumference apart	***badia*** (part) (p. 59)
	Spermathecal pores *c.* 0·5 body circumference apart	***elberti*** (p. 60)

[1] It is uncertain whether the unique type of *P. sibogae* is proandric or metandric. This species has therefore been keyed out to allow for either condition.

[2] *Pheretima cupreae* Chen, 1946 (species incertae sedis) will also emerge at this dichotomy. It may be distinguished from *annulata* by the arrangement of its genital markings (the distribution of this taxon is also different).

[3] *Pheretima touranensis* Michaelsen, 1934*c* (species incertae sedis) will key out at this point. It may be distinguished from *taprobanae* by the possession of two pairs of spermathecal pores (in furrows 7/8/9).

[4] *Planapheretima subulata* closely resembles some species of *Polypheretima*, especially in the form of the genital markings and male pores, so it has been included here to aid differentiation.

[5] *Archipheretima picta* will key out at this point. The male pores and genital markings of this species closely resemble those of *Polypheretima*, and confusion may occur when dealing with individuals lacking fully developed clitella and spermathecal diverticula.

[6] *Pheretima flabellifera* Cognetti, 1911 (species incertae sedis) will key out at this point. It may be distinguished from *brevis* only by the possession of genital markings and small testes sacs.

[7] Although *Polypheretima badia* is diagnosed as possessing spermathecal pores in furrows 5/6/7/8/9 and occasionally 4/5, there are discrepancies between the type series and the original description. The latter reported individuals with spermathecal pores in furrows 6/7/8/9 only, such individuals will emerge at this dichotomy.

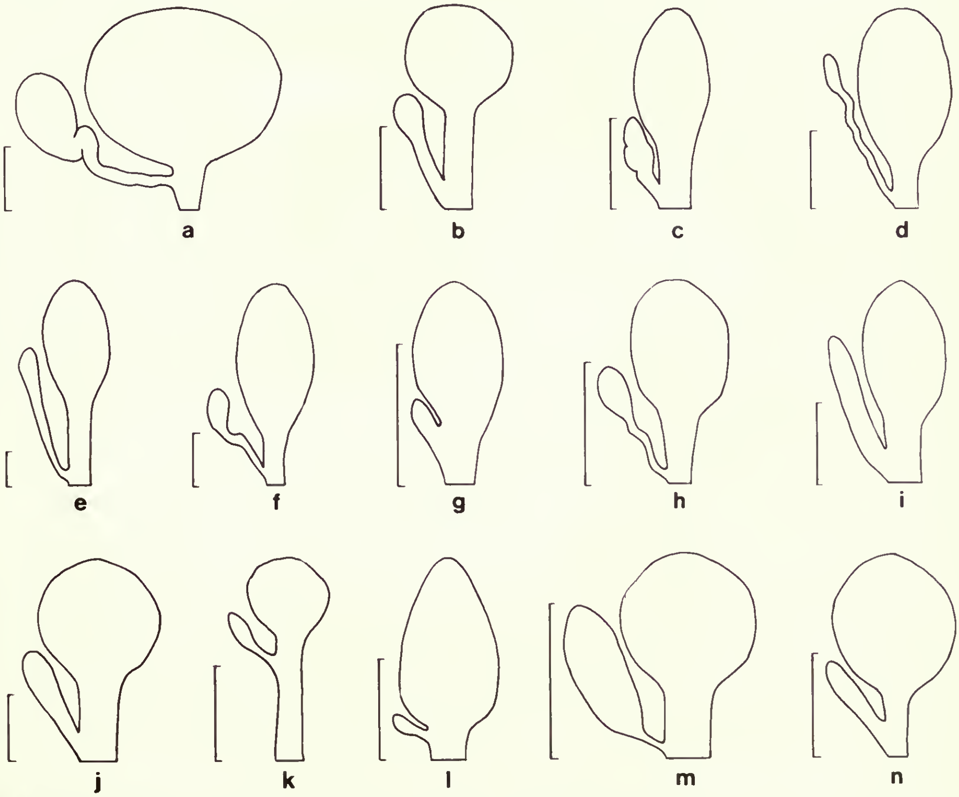

Fig. 15 Spermathecae. (a) *Polypheretima pentacystis*; (b) *P. polytheca*; (c) *P. koyana*; (d) *P. lesonea* sp. nov.; (e) *P. everetti*; (f) *P. aringeana*; (g) *P. annamensis*; (h) *P. sibogae*; (i) *P. elberti*; (j) *P. swelaensis*; (k) *P. patae* sp. nov.; (l) *P. coplandi* sp. nov.; (*m*) *P. kershawae* sp. nov.; (n) *P. huonensis* sp. nov. All scales 0·5 mm.

Polypheretima annulata species-complex

DIAGNOSIS. *Polypheretima* with simple male pores; paired presetal spermathecal pores on *vii* and *viii* or *vii*, *viii* and *ix*.

DESCRIPTION. *External characters.* Length 58–195 mm, diameter 3–7 mm. 56–146 segments. Clitellum *xiv–xvi*. First dorsal pore 10/11–13/14. Setae, 45–72 on *vii*, 50–90 on *xx*, setal ring regular ($aa=ab=yz=zz$).

Male pores on small porophores 0·25–0·28 body circumference apart. Female pore single. Spermathecal pores paired, presetal on *vii* and *viii* or *vii*, *viii* and *ix*, 0·45–0·50 body circumference apart.

Genital markings (Fig. 17a), small, paired, postsetal on *vii*, *viii*, *ix*, two pairs of presetal and two pairs of postsetal markings on *xvii–xix*, lateral pairs slightly median to the line of the male pores. *Internal characters.* Septa 5/6/7/8 thickened, 8/9 membranous or slightly thickened, 9/10–12/13 thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs paired, extending to the dorsal line in *x* and *xi*, seminal vesicles small in *xi* and *xii*, pseudoseminal vesicles in *xiii*, large. Spermathecae (Fig. 14a) paired in *vii–viii* or *vii–ix*.

DISTRIBUTION. (Fig. 16.) West and southwest New Guinea and the islands to the southwest.

REMARKS. The *P. annulata* species-complex is readily recognized by the segmental position of the spermathecal pores. Only one other species of this genus, *voeltzkowi*, has segmental spermathecal pores but they are postsetal on *v*.

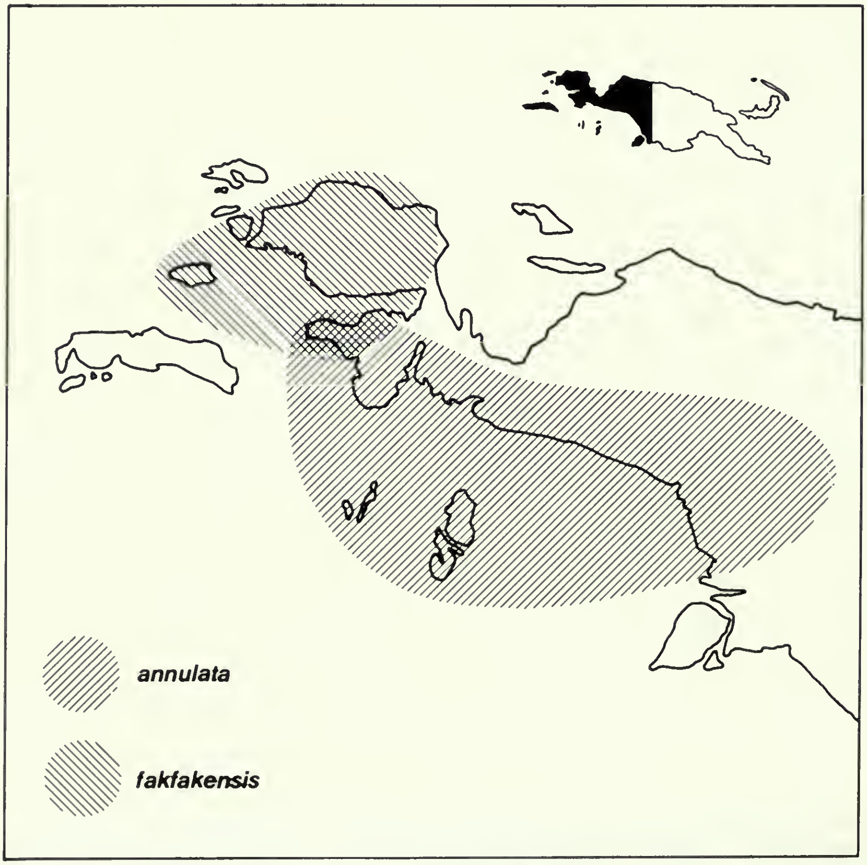

Fig. 16 *Polypheretima annulata* species complex: geographical distribution of the component species.

The two species included are separable on the number of pairs of spermathecae:

P. annulata, characterized by the presence of spermathecae opening onto *vii* and *viii*, occurs in the south-eastern part of the range of the species-complex while *P. fakfakensis* with spermathecae opening onto *vii*, *viii* and *ix*, occurs in the northwestern portion of the range.

The close affinity of these two species was first recognized by Michaelsen (1910*a*) when he described *fakfakensis tetratheca*, which is here included in the synonymy of *annulata* together with *kochii* and its synonyms *invisa* and *schaedleri* (Michaelsen, 1938).

Polypheretima annulata (Horst, 1883)

Megascolex annulatus Horst, 1883 : 195.
Perichaeta annulata: Horst, 1890 : 236; Horst, 1893 : 29; Beddard, 1895 : 426.
Amynthas annulatus: Beddard, 1900*a* : 634.
Pheretima annulata: Michaelsen, 1900 : 253.
Metapheretima annulata: Sims & Easton, 1972 : 233.
Pheretima fakfakensis tetratheca Michaelsen, 1910*a* : 254; Michaelsen, 1922 : 53; Michaelsen, 1930*b* : 13; Gates, 1936*b* : 385.
Metapheretima fakfakensis tetratheca: Sims & Easton, 1972 : 233.
Pheretima kochii Cognetti, 1913 : 293.
Pheretima (*Pheretima*) *kochii*: (syn. *invisa*, *schaedleri*) Michaelsen, 1938 : 167.
Metapheretima kochii: Sims & Easton, 1972 : 233.
Pheretima invisa Cognetti, 1913 : 294.

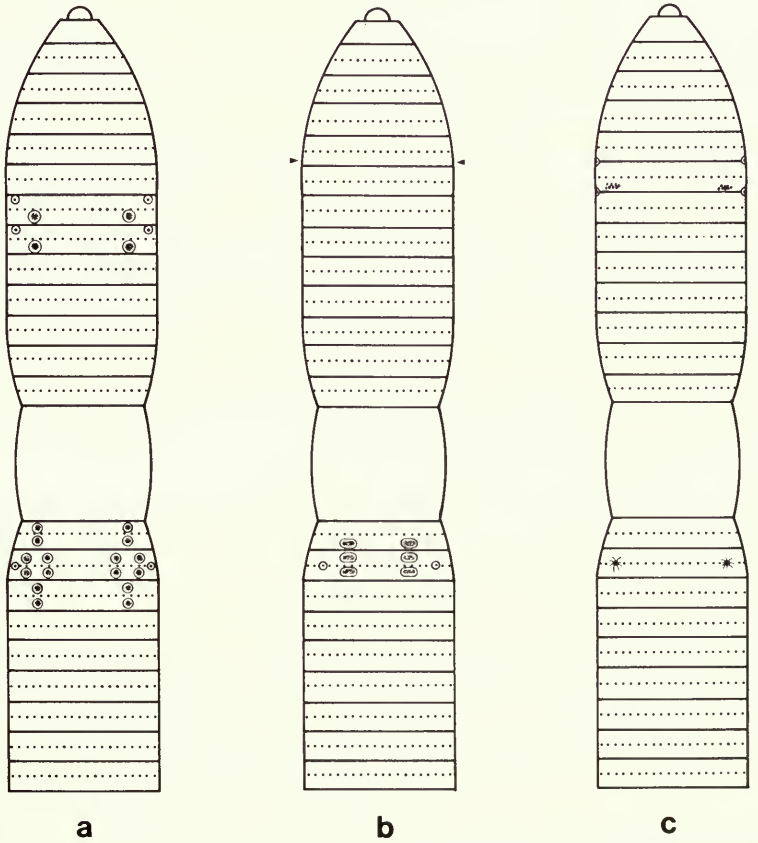

Fig. 17 Anterior ventral surface, diagnostic characters. (a) *Polypheretima annulata*; (b) *P. voeltzkowi*, arrows indicate dorsal postsetal spermathecal pores; (c) *P. grata*.

Metapheretima invisa: Sims & Easton, 1972 : 233.
Pheretima schaedleri Michaelsen, 1922 : 52.
Metapheretima schaedleri: Sims & Easton, 1972 : 233.

DIAGNOSIS. *P. annulata* species-complex with spermathecal pores on segments *vii* and *viii*.

DISTRIBUTION. Southwest New Guinea, Kepulauan Banda, Kepulauan Kai, Kepulauan Aru.

MATERIAL EXAMINED. 2C 'Indonesia'; Leiden 1855 (syntypes of *annulata*). 4C Gt Kai, Kepulauan Kai; Hamburg v3032 (syntypes of *fakfakensis tetratheca*). 1C Gt Kai, Kepulauan Kai; Bogor Ann058 (*fakfakensis tetratheca*: Gates, 1936). 2C, 1A Etna Bay, West Irian; Amsterdam Vol. 275 (syntypes of *kochii*). 1C Bivak Island, West Irian; Hamburg v11729 (*kochii*: Michaelsen, 1938, other specimens of this series, Amsterdam Vol. 278, were not examined). 1C Sabang, West Irian; Amsterdam Vol. 270 (syntype of *invisa*). 1C Skroë, West Irian; Leiden 1822 (holotype of *schraedleri*).

OTHER RECORDS. Wammer Island, Kepulauan Aru (syntype(s) of *fakfakensis tetratheca*). Kobroor Island, Kepulauan Aru (syntype(s) of *fakfakensis tetratheca*). Dobo, Kepulauan Aru; Leiden 1815 (*fakfakensis tetratheca*: Michaelsen, 1922). Kepulauan Aru (*fakfakensis tetratheca*: Michaelsen 1930). Near river Lorentz, West Irian (syntype of *kochii*). Bivak Island and north of river Lorentz, West Irian (syntypes of *invisa*).

Polypheretima fakfakensis (Cognetti, 1908)

Pheretima fakfakensis Cognetti, 1908 : 1.
Pheretima (*Pheretima*) *fakfakensis*: Michaelsen, 1930*b* : 12.
Metapheretima fakfakensis: Sims & Easton, 1972 : 233.

DIAGNOSIS. *P. annulata* species-complex with spermathecal pores on segments *vii*, *viii* and *ix*.

DISTRIBUTION. Western New Guinea; Misoöl Island.

REMARKS. Preclitellar genital markings are present on *viii* and *ix* (*vii* and *viii* in *P. annulata*) in the specimens examined.

MATERIAL EXAMINED. *Previously reported.* 2C Fakfak, West Irian; BMNH 1908.5.12.1–2 (syntypes of *fakfakensis*). 1C Misoöl Islands, West Irian; Hamburg v11638 (*fakfakensis*: Michaelsen, 1930, reported from a long series but the present location of the other individuals in unknown). *New record.* 2C, 1A Vogelkop, West Irian; Leiden.

Polypheretima bifaria species-group

DIAGNOSIS. *Polypheretima* with simple male pores; intersegmental spermathecal pores. Holandric.

DISTRIBUTION. Indigenous species occur throughout the *Pheretima* domain. Three species, *brevis*, *fida* and *taprobanae*, are known only from localities to which they are suspected of being introduced.

SPECIES INCLUDED. *bifaria*, *brevis*, *fida*, *gatesi*, *iizukai*, *mertoni*, *moelleri*, *monticola*, *panarana*, *sempolensis*, *sepikensis*, *taprobanae*.

REMARKS. Several morphological trends may be detected among the species assigned to this group. The Asian representatives have only a single pair of genital markings on each of several segments while those from the Papuan region have more numerous genital markings restricted to one or two segments near the male pores (see also *annulata* species-complex and the *patae* species-group). The glands associated with the genital markings in all Asian and most Papuan species are restricted to the body wall but those of species from the north eastern part of New Guinea are stalked and conspicuous (see also the Papuan species *grata*). This species-group is proposed for convenience of identification.

Marker characters of the species included in the *bifaria* species-group are given in Table 6.

Table 6 Marker characters of the members of the *Polypheretima bifaria* species-group

Species	Spermathecal furrows	Separation of spermathecal pores	Postclitellar genital markings	Indigenous distribution
fida	4/5/6 or 4/5/6/7	0·50	1 pair pre- and postsetal *xvii*, *xix* (Fig. 18a)	? Loyalty Is.
moelleri	4/5/6/7/8/9	?	?	Java
sempolensis	5/6/7	0·33	1 pair *xvii*, *xix* (Fig. 18b)	Java
mertoni	5/6/7	0·40	1 pair pre- and postsetal and single median presetal *xvii–xix* (Fig. 18c)	Aru Islands
sepikensis	5/6/7	0·33	numerous, random on *xviii* stalked glands present (Fig. 18d)	North east New Guinea
brevis	5/6/7/8	0·53	?	? Christmas Island (Indian Ocean)
bifaria	5/6/7/8 or 5/6/7/8/9	0·33 (polythecal)	2 pairs pre- and postsetal *xviii*, 1 pair *xvii*, *xix* (Fig. 19a)	North west New Guinea
monticola	5/6/7/8/9	?	1 pair presetal, *xvii*, *xix–xx* (Fig. 19b)	Philippines
iizukai	5/6/7/8/9	?	1 pair postsetal *xix–xxiii* (Fig. 19c)	Japan
gatesi	6/7	0·51	numerous, random on *xviii* (Fig. 20a)	East New Guinea
panarana	6/7	0·30	numerous in clusters round ♂ pores stalked glands present (Fig. 20b)	West New Guinea
taprobanae	7/8	0·50	1 pair presetal *xix–xxii* (Fig. 20c)	?

Polypheretima fida (Michaelsen, 1913)

Pheretima fida Michaelsen, 1913*b* : 259.
Metapheretima fida: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with simple male pores; spermathecal pores in furrows 4/5/6 and occasionally 6/7. Holandric.

DESCRIPTION. *External characters.* Length 40–60 mm, diameter 4–5 mm. 93–98 segments. Clitellum *xiv*–½*xvi*. First dorsal pore 10/11. Setae, 40–50 on *vii* and *xx*, setal ring regular with ventral gaps ($aa = 1{\cdot}5ab = 1{\cdot}5yz = 1{\cdot}5zz$).

Male pores on circular porophores, occasionally slightly invaginated, *c.* 0·30 body circumference apart. Female pores paired. Spermathecal pores paired, intersegmental in 4/5/6 and occasionally 6/7, *c.* 0·50 body circumference apart.

Genital markings (Fig. 18a) simple, paired, presetal on *xi–xiii* slightly median to the line of the spermathecal pores, pre and postsetal on *xvii* and *xix* in line with the male pores.

Internal characters. Septa 4/5–6/7 thickened, 7/8–8/9 absent, 9/10–11/12 thickened. Intestine begins in *xv*. Lateral hearts in *x–xii*.

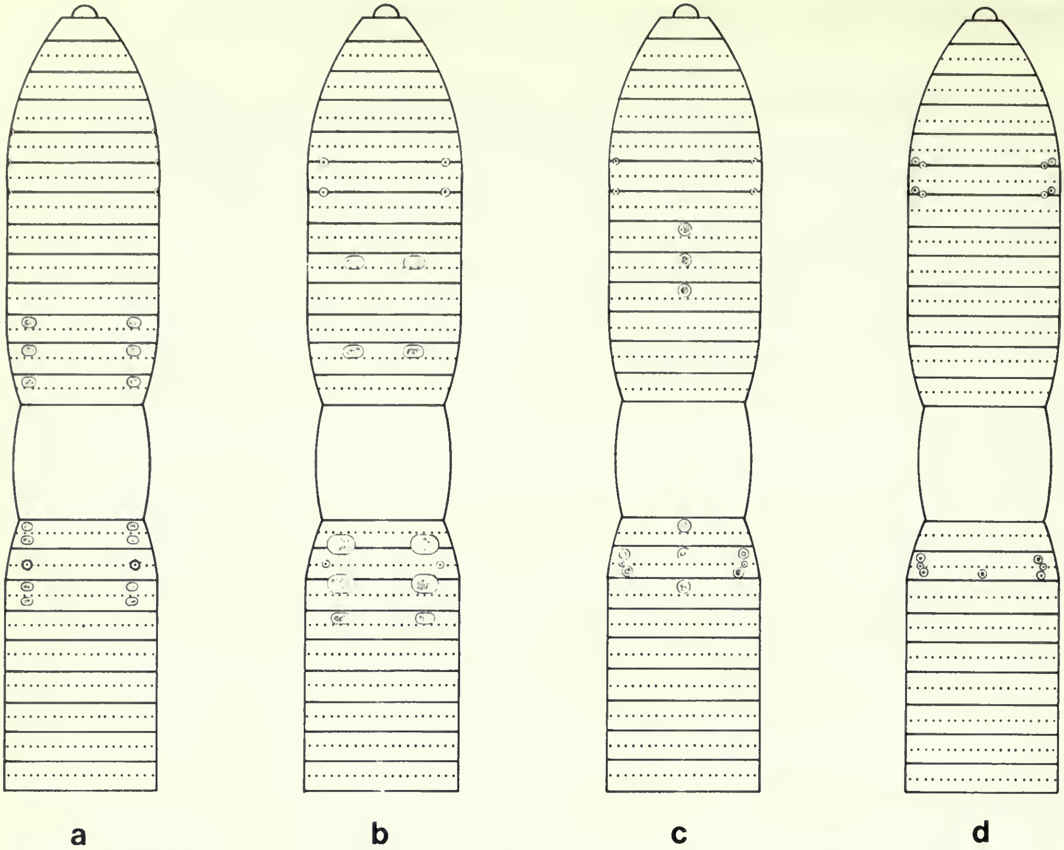

Fig. 18 Anterior ventral surface, diagnostic characters. (a) *Polypheretima fida*; (b) *P. sempolensis* sp. nov.; (c) *P. mertoni*; (d) *P. sepikensis*.

Holandric, testes sacs annular in *x* and *xi*, enclosing the lateral hearts and in *xi* the seminal vesicles, seminal vesicles large, reaching the dorsal line in *xi* and *xii*. Pseudoseminal vesicles absent. Spermathecae (Fig. 14b) paired in *v*, *vi*, and occasionally in *vii*.

DISTRIBUTION. Loyalty Islands.

REMARKS. The only record of *fida* is based on the type series collected in the Loyalty Islands which are only tentatively included within the *Pheretima* domain (see above). As the five other representatives which have been recorded from the Loyalty Islands and nearby New Caledonia (*Amynthas diffringens*, *A. rodericensis*, *A. taitensis*, *Pheretima montana* and *Polypheretima elongata*) are all peregrine species (Michaelsen, 1913*b*) the occurrence of *fida* in this area is also probably the result of introduction by man. Possible evidence for *fida* being indigenous in this area is its low affinities (see numerical studies) with other species of the *bifaria* species-group.

MATERIAL EXAMINED. 5C Lifu, Loyalty Islands; Hamburg v8067 (syntypes of *fida*). 4C Uvea, Loyalty Islands; Hamburg v8068 (syntypes of *fida*).

Polypheretima moelleri (Michaelsen, 1921)

Pheretima mölleri Michaelsen, 1921 : 12.
Metapheretima moelleri: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with simple male pores; paired spermathecal pores in furrows 4/5/6/7/8/9. Holandric.

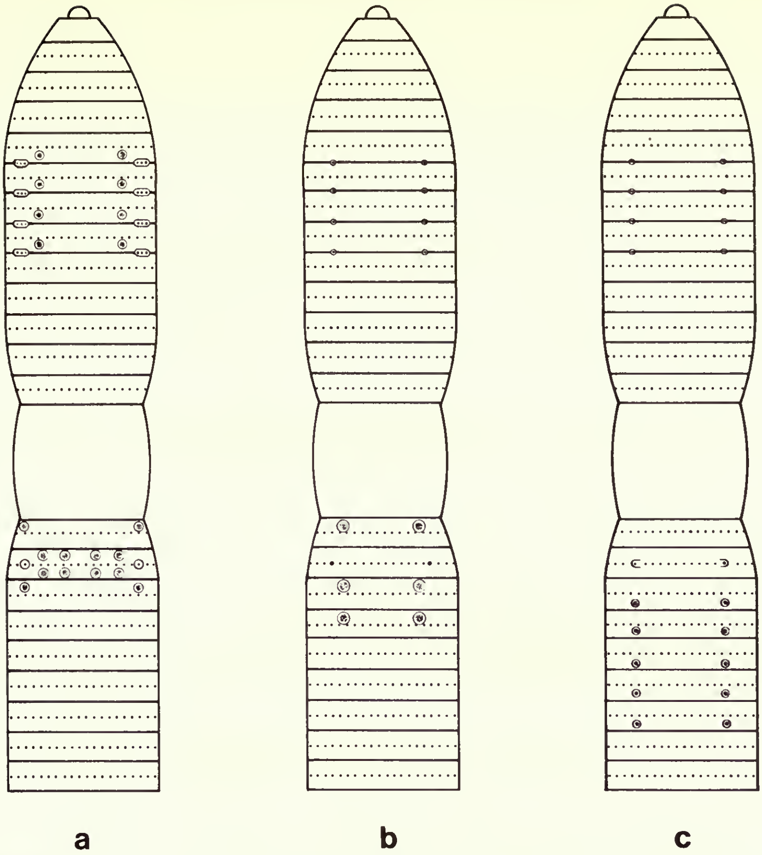

Fig. 19 Anterior ventral surface, diagnostic characters. (a) *Polypheretima bifaria*; (b) *P. monticola*; (c) *P. iizukai*.

Description. *External characters*. Length over 24 mm, diameter *c*. 1·3 mm. Over 41 segments. (The unique holotype lacks a posterior portion.) Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, *c*. 24 on *ii*, *c*. 30 on *iii*, *c*. 40 on *viii*, *c*. 36 on *xxvi*, setal ring with ventral gaps (*aa*=1–1·3*ab*).

Male pores simple, on large hemispherical porophores, *c*. 0·40 body circumference apart. Female pore(s) not recorded. Spermathecal pores paired, intersegmental in 4/5/6/7/8/9, separation not recorded.

Genital markings absent.

Internal characters. Anterior septa delicate, 7/8 absent. Beginning of intestine not recorded. Lateral hearts not recorded.

Holandric, testes sacs large, paired in *x* and *xi*, seminal vesicles in *xi* and *xii*. Spermathecae (Fig. 14c) paired in *v–ix*.

Description after Michaelsen (1921).

Distribution. Java.

Remarks. It has not been possible to locate any examples of this species and *moelleri* is only tentatively assigned to *Polypheretima* in the absence of any of the characteristics diagnostic of other acaecate genera (none of which has been recorded from Java).

Records. 1C (incomplete) Sand Bay, south coast of Java (holotype of *moelleri*).

Polypheretima sempolensis sp. nov.

Diagnosis. *Polypheretima* with simple male pores; paired spermathecal pores in furrows 5/6/7. Holandric. Postclitellar genital markings simple, postsetal on *xvii*, presetal on *xix*.

DESCRIPTION. *External characters*. Length 50–62 mm, diameter *c*. 2 mm. 100–107 segments. Clitellum *xiv–xvi*. First dorsal pore 13/14. Setae, *c*. 60–66 on *vii*, 44–48 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores simple on porophores, *c*. 0·33 body circumference apart. Female pore single. Spermathecal pores paired, intersegmental in 5/6/7, *c*. 0·33 body circumference apart.

Genital markings (Fig. 18b) simple paired, presetal on *ix*, *xii* and occasionally *xiii*, median to the line of the spermathecal pores, postsetal on *xvii*, presetal on *xix* and occasionally *xx*, median to the line of the male pores. The genital markings are exceptionally large, invading the setal lines and the intersegmental furrows.

Internal characters. Septa 5/6–7/8 thickened, 8/9/10 membranous, 10/11–12/13 thickened. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Holandric, testes sacs on *x* separated ventrally but linked dorsally, that of *xi* annular and enclosing the anterior seminal vesicles, seminal vesicles slim, elongate, reaching the dorsal line in *xi* and *xii*, pseudoseminal vesicles small in *xiv*. Spermathecae (Fig. 14d) paired in *vi* and *vii*.

DISTRIBUTION. East Java, 1400–1500 m.

MATERIAL EXAMINED. 3C Primary forest with rich black soil tending to be rather dry, on top of ridge of ancient crater wall, Sempol Crater, East Java, 8° 03′ S, 114° 12′ E, 1500 m, *coll* G A Lincoln 29 Jul 1973 British University Dragon Expedition; BMNH 1975.7.48–50 (syntypes of *sempolensis*). 11C, 7A Loose black soil in middle of coffee plantation, plateau of Gunung Raung, Sempol, East Java, 1400 m, *coll* G A Lincoln 27 Jul 1973 British University Dragon Expedition; BMNH 1975.7.28–47.

Polypheretima mertoni (Michaelsen, 1910)

Pheretima mertoni Michaelsen, 1910*a* : 256.
Metapheretima mertoni: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with simple male pores; paired spermathecal pores about two fifths of the body circumference apart in furrows 5/6/7. Holandric. Postclitellar genital markings single presetal median and paired, pre- and postsetal close to the line of the male pores.

DESCRIPTION. *External characters*. Length 36–58 mm, diameter 2–2·5 mm. 76–82 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13 or 13/14. Setae, *c*. 44 on *vii*, *c*. 40 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores simple *c*. 0·30 body circumference apart. Female pore single. Spermathecal pores paired, intersegmental in 5/6/7, *c*. 0·40 body circumference apart.

Genital markings (Fig. 18c), single median, presetal on *viii*, *ix*, *xvii–xix*, paired, pre- and postsetal, close to the line of the male pores on *xviii*.

Internal characters. Septa 5/6/7 slightly thickened, 7/8–13/14 membranous. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Holandric, testes sacs paired with narrow ventral connections, large, extending to the dorsal line in *x* and *xi*, seminal vesicles large, extending to the dorsal line in *xi* and *xii*, those of *xi* enclosed in the testes sacs. Spermathecae (Fig. 14e) paired in *vi* and *vii*.

DISTRIBUTION. Kepulauan Aru.

MATERIAL EXAMINED. 3C Wokam, Aru Kepulauan; Hamburg v3035 (syntypes of *mertoni*).

Polypheretima sepikensis (Ude, 1924)

Pheretima sepikensis Ude, 1924 : 81.
Pheretima (*Pheretima*) *sepikensis*: Ude, 1932 : 135.
Metapheretima sepikensis: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with simple male pores; paired spermathecal pores about one third of body circumference apart in furrows 5/6/7. Holandric. Postclitellar genital markings simple, randomly arranged on *xviii*, with stalked glands discharging into them.

DESCRIPTION. *External characters*. Length 40–60 mm, diameter 2–3 mm. 100–120 segments. Clitellum *xiv–xvi*. First dorsal pore 5/6. Setae, 48–50 on *vii*, 44–48 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores on small circular porophores *c.* 0·33 body circumference apart. Female pore single. Spermathecal pores paired, intersegmental in 5/6/7, *c.* 0·33 body circumference apart.

Genital markings (Fig. 18d) small, paired, postsetal on *v* and *vi*, slightly lateral to the spermathecal pores, small, numerous, randomly arranged on *xviii*.

Internal characters. Septa 5/6–13/14 slightly thickened. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Holandric, testes sacs large, paired, extending to the dorsal line in *x* and *xi*, seminal vesicles extending to the dorsal line in *xi* and *xii*, those of *xi* enclosed in the testes sacs. Spermathecae (Fig. 14f) paired in *vi* and *vii*.

Stalked glands discharge through the genital markings associated with the male pores and spermathecal pores.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 9C, 4A Sepik area, Papua New Guinea; Berlin 6471 (syntypes of *sepikensis*).

Polypheretima brevis (Rosa, 1898)

Perichaeta brevis Rosa, 1898*a* : 288.
Amynthas brevis: Beddard, 1900*a* : 636.
Pheretima brevis: Michaelsen, 1900 : 257.
Metapheretima brevis: Sims & Easton, 1972 : 180, 233.

DIAGNOSIS. *Polypheretima* with simple male pores; paired spermathecal pores about half body circumference apart in furrows 5/6/7/8. Holandric.

DESCRIPTION. *External characters*. Length 15–20 mm, diameter 1·5–2·5 mm. 70–80 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13 or 13/14. Setae, 48–52 on *vii*, 40–50 on *xx*, setal ring regular on preclitellar segments ($aa = ab = yz = zz$), with ventral gaps on postclitellar segments ($aa = 1{\cdot}5ab = 1{\cdot}5yz = 1{\cdot}5zz$).

Male pores simple, on small circular porophore *c.* 0·28 body circumference apart. Female pore single. Spermathecal pores paired, intersegmental in 5/6/7/8, *c.* 0·53 body circumference apart.

Genital markings absent.

Internal characters. Septa 5/6–13/14 membranous. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Holandric, testes sacs paired, those of *x* large, extending to the dorsal line, those of *xi* small, ventral, seminal vesicles in *xi* and *xii*, extending to the dorsal line. Pseudoseminal vesicles in *xiii*. Spermathecae (Fig. 14g) paired in *vi–viii*.

DISTRIBUTION. Christmas Island, Indian Ocean.

REMARKS. *P. brevis* is known only from Christmas Island in the Indian Ocean. The oceanic nature of this island suggests that the record of *brevis* is the result of introduction through the agency of man. The affinities of *brevis* with the Papuan representatives of the *bifaria* species-group (see numerical studies) may indicate that it is indigenous in the New Guinea area.

None of the three syntypes possess genital markings, but when more material becomes available it is possible that markings will be found similar to those of *bifaria*.

MATERIAL EXAMINED. 3C Christmas Island, Indian Ocean; BMNH 1898.10.28.1–2 (syntypes of *brevis*).

Polypheretima bifaria (Michaelsen, 1924)

Pheretima bifaria Michaelsen, 1924 : 18.
Pheretima (*Polypheretima*) *bifaria*: Michaelsen, 1934*b* : 16.
Pheretima (*Polypheretima*) *bifaria typica*: Michaelsen, 1938 : 171.
Metapheretima bifaria bifaria: Sims & Easton, 1972 : 233.
Pheretima (*Polypheretima*) *bifaria wirzi* Michaelsen, 1938 : 171.

Metapheretima bifaria wirzi: Sims & Easton, 1972 : 233.
? *Pheretima polytheca aruensis* Michaelsen, 1910*a* : 252.
? *Pheretima* (*Polypheretima*) *polytheca aruensis*: Michaelsen, 1934*b* : 16.
? *Metapheretima polytheca aruensis*: Sims & Easton, 1972 : 233.

Diagnosis. *Polypheretima* with simple male pores; numerous spermathecal pores in paired batteries in furrows 5/6/7/8 and usually 8/9. Holandric. Postclitellar genital markings, two pairs of presetal and two pairs of postsetal markings on each segment.

Description. *External characters.* Length 27–49 mm, diameter 1·5–2·5 mm. 99–110 segments. Clitellum *xiv–xvi*. First dorsal pore 11/12 or 12/13. Setae, 33–45 on *vii*, 32–40 on *xx*, setal ring regular with dorsal and ventral gaps ($aa = 1{\cdot}5\text{–}2ab = 2yz = zz$).

Male pores simple on large porophores 0·30–0·33 body circumference apart. Female pore single. Spermathecal pores numerous in paired intersegmental batteries of 1–3 pores in 5/6/7/8 and usually 8/9, *c.* 0·30 body circumference apart.

Genital markings (Fig. 19a), simple, single median or closely paired pre- or postsetal on *v–ix*, paired, presetal in line with the male pores, on *xvii* and *xix*, two pairs of presetal and two pairs of postsetal, on *xviii* median to the male pores.

Internal characters. Septa 5/6–7/8 thickened, 8/9 membranous, 9/10–12/13 thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs paired, extending to the dorsal line in *x* and *xi*, seminal vesicles extending to the dorsal line in *xi* and *xii*, those of *xi* are enclosed in testes sacs. Spermathecae (Fig. 14h) numerous in paired batteries of 1–3 spermathecae in *vi*, *vii*, *viii* and usually *ix*.

Distribution. New Guinea and possibly Kepulauan Aru.

Remarks. Michaelsen (1938) recognized two subspecies of *bifaria*, one with single and the other with paired preclitellar genital markings. It is considered that these differences indicate individual variation and that they do not provide the means of recognizing subspecies.

The type series of *polytheca aruensis* could not be located during the preparation of this paper, but from the original description it appears to be closely allied to *bifaria* and differs considerably from the nominate subspecies of *polytheca* (known only from Malaya).

Material examined. 3C Doormanpad-biwak, West Irian; Hamburg v9400 (syntypes of *bifaria bifaria*). 2C Panarana-del, West Irian; Amsterdam Vol. 247 (*bifaria typica*: Michaelsen, 1938). 1C Panarana-del, West Irian; Amsterdam Vol. 246 (holotype of *bifaria wirzi*).

Other records. ? –, Kobroor, Aru Kepulauan (type(s) of *polytheca aruensis*).

Polypheretima monticola (Beddard, 1912)

Pheretima monticola Beddard, 1912: 195.
Metapheretima monticola: Sims & Easton, 1972 : 233.

Diagnosis. *Polypheretima* with simple male pores; paired spermathecal pores in furrows 5/6/7/8/9. Holandric. Postclitellar genital markings simple, paired, presetal.

Description. *External characters.* Length *c.* 130 mm, diameter *c.* 7 mm. Segment number not recorded. Clitellum *xiv–xvi*. Position of first dorsal pore not recorded. Setal numbers not recorded.

Male pores 'conspicuous', widely separated. Condition of female pore(s) not recorded. Spermathecal pores paired in 5/6/7/8/9, separation not recorded.

Genital markings (Fig. 19b) large, circular or oval, presetal, paired markings on *ix*, *xvii*, *xix–xx*, slightly median to the line of the male pores.

Internal characters. All anterior septa present, 9/10–12/13 thickened. Intestine begins in *xv*. Segments with lateral hearts not recorded.

Holandric, testes in *x* and *xi*, either free or in large delicate sacs, seminal vesicles in *xi* and *xii*. Spermatheca paired in *vi–ix*, duct short, ampulla spherical, diverticulum long and convoluted, terminating in a small spherical ampulla.

Description after Beddard, 1912; Fig. 19b is an interpretation of the genital field based on the written description.

DISTRIBUTION. Luzon, Philippines.

REMARKS. Beddard's original description lacked detailed information and since the type series cannot be located, this species is tentatively assigned to the genus *Polypheretima* where it is placed provisionally in the *bifaria* species-group. (The clitellum extends over only three segments and the spermathecal diverticula are apparently simple.)

At present *monticola* is unique in being the only indigenous species of *Polypheretima* from the Philippines.

RECORDS. 2 specimens, Mt Pulong, Luzon, Philippines (syntypes of *monticola*).

Polypheretima iizukai (Goto & Hatai, 1899)

Perichaeta iizukai Goto & Hatai, 1899 : 14.
Amynthas iizukai: Beddard, 1900*a* : 625.
Pheretima iizukai: Michaelsen, 1900 : 274; Ohfuchi, 1937 : 39; Kobayashi, 1941*a* : 260, 266; Kobayashi, 1941*b* : 380, 381.
Metapheretima iizukai: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with simple male pores; paired spermathecal pores in furrows 5/6/7/8/9. Holandric. Postclitellar genital markings paired, postsetal.

DESCRIPTION. *External characters*. Length *c*. 235 mm, diameter 12–15 mm. *C*. 137 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, *c*. 34 on *iv*, *c*. 40 on *v*, *c*. 42 on *vi*, *c*. 50 on *viii*, *c*. 60 on posterior segments. Setal ring regular.

Male pores simple, *c*. 8 setae apart. Female pore(s) not recorded. Spermathecal pores paired, intersegmental in 5/6/7/8/9, separation not recorded.

Genital markings (Fig. 19c) paired, postsetal, in line with the male pores on *xix–xxiii*.

Internal characters. Septa 4/5–7/8 thickened, 8/9/10 absent, 10/11–12/13 thickened. Intestine begins in *xv*. Last lateral hearts in *xiii*.

Holandric, testes sacs in *x* and *xi*, seminal vesicles in *xi* and *xii*, no other details recorded. Spermathecae (Fig. 14i) paired in *vi–ix*.

Description after Goto & Hatai (1899).

DISTRIBUTION. Japan.

REMARKS. *P. iizukai* is the only representative of *Polypheretima* recorded from Japan where it occurs at the northernmost limit of the genus. Two other Japanese species, *Amynthas fuscatus* (Goto & Hatai, 1898) and *Metaphire grossa* (Goto & Hatai, 1898), have postsetal genital markings and spermathecal pores in furrows 5/6/7/8/9 and may be confused with *iizukai*. However, they are readily distinguishable by the presence of intestinal caeca.

Although the earthworm fauna of Japan has received considerable attention prior to 1940, this species has been recorded only four times. Of these recorded, one (Ohfuchi, 1937) is suspect since Ohfuchi noted (p. 41) 'intestinal caeca present' although earlier (p. 39) he had accurately repeated the original description. Kobayashi (1941*a* & *b*) recorded this species from only two mountainous districts of central Honshu. The absence of other acaecate species from Japan and from the adjacent Asian mainland may indicate that *iizukai*, by now being confined to mountainous refuges, is a relict from a time when *Polypheretima* was more widespread in Asia.

RECORDS. 1C Musashi, Japan (holotype of *iizukai*, at one time contained in the collections of the University of Tokyo but it could not be located during the preparation of this paper: Dr M. Imajima, private communication). Near Tokyo, Japan (? *iizukai*: Ohfuchi, 1937). Chubu & Kanto districts, Japan (*iizukai*: Kobayashi, 1941*a* & *b*, it is uncertain whether these are new records since both papers are in Japanese).

Polypheretima gatesi sp. nov.

? *Pheretima panarana*: Gates, 1948 : 159 (non Michaelsen, 1938 : 167).

DIAGNOSIS. *Polypheretima* with simple male pores; paired spermathecal pores about half body circumference apart in furrow 6/7. Holandric. Postclitellar genital markings numerous in irregular presetal and postsetal rows.

DESCRIPTION. *External characters.* Length 49–54 mm – the two syntypes of this species are both aclitellate, mature specimens may be considerably larger – diameter *c.* 2 mm. 63–71 segments. Clitellum not recognizable. First dorsal pore 12/13. Setae, 20–24 on *vii*, 36–40 on *xx*, setal ring regular with dorsal and ventral gaps (*aa*=2*ab*=2*yz*=*zz*).

Male pores simple on circular porophores *c.* 0·35 body circumference apart. Female pore(s) not detected. Spermathecal pores paired, intersegmental in 6/7, *c.* 0·51 body circumference apart.

Genital markings (Fig. 20a) numerous, irregularly arranged, pre and postsetal on *xviii*, presetal on *xix*.

Internal characters. Septa 5/6–13/14 membranous. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs paired, those of *x* extending to the dorsal line, those of *xi* small, ventral, seminal vesicles large, extending to the dorsal line in *xi* and *xii*. Pseudoseminal vesicles in *xiii*. Spermathecae (Fig. 14j) paired in *vii*.

DISTRIBUTION. New Guinea.

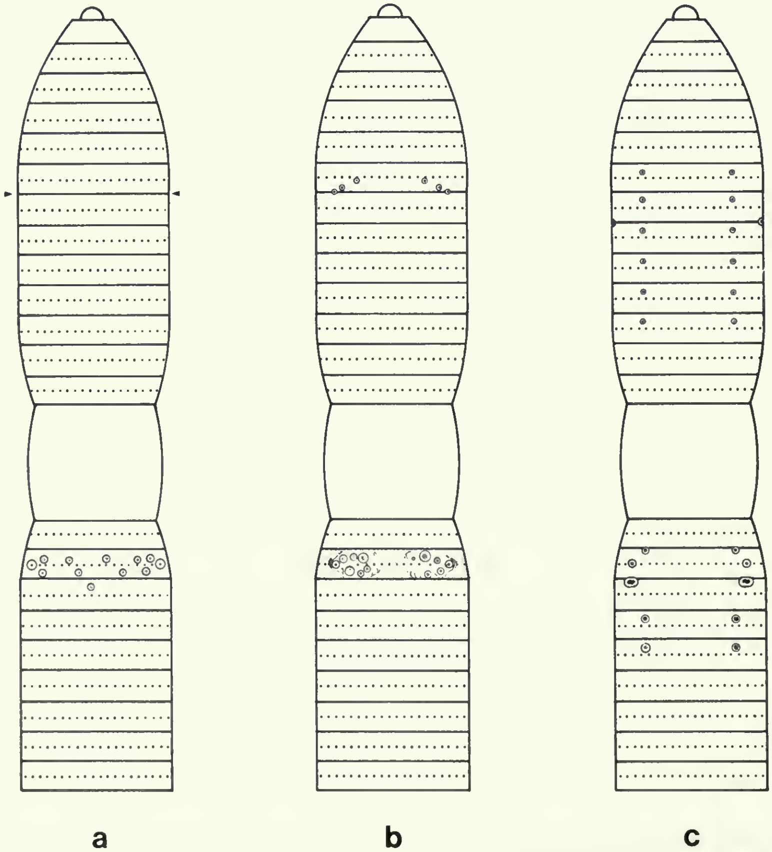

Fig. 20 Anterior ventral surface, diagnostic characters. (a) *Polypheretima gatesi* sp. nov., arrows indicate furrows with dorsal spermathecal pores; (b) *P. panarana*; (c) *P. taprobanae*.

REMARKS. The specimen identified as *panarana* by Gates (1948) has been tentatively assigned to this taxon principally because of the greater separation described between the spermathecal pores than is found in *panarana* sensu stricto.

MATERIAL EXAMINED. 2A Local government piggery, Wabag, Mt Hagen, District, Western Highlands, Papua New Guinea, 5° 28′ S, 143° 40′ E, *coll* J W Copland; BMNH 1976.3.184–185 (syntypes of *gatesi*).

OTHER RECORDS. ? 1C Mt Wilhelmina, West Irian (*panarana*: Gates, 1948).

Polypheretima panarana (Michaelsen, 1938)

Pheretima (*Pheretima*) *panarana* Michaelsen, 1938 : 167.
[non *Pheretima panarana*: Gates, 1948 : 159 (?=*P. gatesi*)]
Metapheretima panarana: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with simple male pores; paired spermathecal pores about one third body circumference apart in furrow 6/7. Holandric. Postclitellar genital markings in paired clusters associated with the male pores.

DESCRIPTION. *External characters*. Length *c*. 31 mm, diameter *c*. 2·5 mm. *c*. 69 segments. Clitellum *xiv–xvi*. First dorsal pore 13/14. Setae, *c*. 43 on *vii*, *c*. 50 on *xx*, setal ring regular (*aa*=*ab*=*yz*=*zz*).

Male pores simple on conical porophores *c*. 0·30 body circumference apart. Female pore single. Spermathecal pores paired, intersegmental in 6/7, *c*. 0·30 body circumference apart.

Genital markings (Fig. 20b), medium sized simple papillae arranged in paired clusters of 2–3 papillae, postsetal on *vii* and presetal on *viii*, median to the spermathecal pores, clusters of up to 5 papillae incorporating the male pores on *xviii*.

Internal characters. Septa 5/6–7/8 membranous, 8/9 absent, 9/10–13/14 membranous. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Holandric, testes sacs large, paired, those of *x* extending to the lateral line and those of *xi* extending to the dorsolateral line, seminal vesicles in *xi* and *xii*, those of *xi* enclosed in the testes sacs, those of *xii* extending to the dorsolateral line. Spermathecae (Fig. 14k) paired in *vii*.

Large glandular masses in *vi* and *vii* adjacent to the genital markings, similar masses in *xviii* around the ectal end of the prostatic duct.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 1C Panarana-del, West Irian; Amsterdam Vol. 292 (holotype of *panarana*).

Polypheretima taprobanae (Beddard, 1892)

Perichaeta taprobanae Beddard, 1892 : 163; Beddard, 1895 : 411; Michaelsen, 1897 : 140.
Amynthas taprobanae: (=*pauli*) Beddard, 1900*a* : 648.
Pheretima taprobanae typica: Michaelsen, 1900 : 308.
Pheretima taprobanae: Michaelsen, 1903*a* : 12; Michaelsen, 1907 : 46; Stephenson, 1923 : 312; Michaelsen, 1927 : 371; Aiyer, 1929 : 15, 72; Gates, 1937*a* : 371; Gates, 1937*b* : 209; Gates, 1945 : 87; Gates, 1972*a* : 220.
Metapheretima taprobaena: Sims & Easton, 1972 : 181, 233.
Perichaeta pauli Michaelsen, 1897 : 243.
Pheretima taprobanae pauli: Michaelsen, 1900 : 309; Moreira, 1903 : 132.
Metapheretima pauli: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with simple male pores; paired spermathecal pores in furrow 7/8. Holandric.

DESCRIPTION. *External characters*. Length 80–145 mm, diameter 4–7 mm. 95–136 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, 70–80 on *vii*, 60–80 on *xx*, setal ring regular with ventral gaps on preclitellar segments (*aa*=1·5*ab*=1·5*yz*–1·5*zz*) and with dorsal and ventral gaps on postclitellar segments (*aa*=2*ab*=2*yz*=0·7*zz*).

Male pores simple on small porophores *c*. 0·29 body circumference apart. Female pore single. Spermathecal pores paired, intersegmental in 7/8, *c*. 0·50 body circumference apart.

Genital markings (Fig. 20c), small, simple, paired, presetal on *vi–ix*, slightly median to the spermathecal pores, presetal on *xviii–xxii*, slightly median to the line of the male pores.
Internal characters. Septa 5/6–7/8 thickened, 8/9 membranous, 9/10 absent, 10/11/12 membranous, 12/13/14 thickened. Intestine begins in *xv*. Lateral hearts *x–xii*.

Holandric, testes sacs annular in *x* and *xi*, enclosing the lateral hearts and, in *xi* the seminal vesicles, seminal vesicles in *xi* and *xii*, extending to the lateral line. Spermathecae (Fig. 14l) paired in *viii*.

DISTRIBUTION. *Introduced records.* Brazil, Madagascar, Seychelles, India, Sri Lanka, Queensland, Fiji, Hawaii.

REMARKS. *P. taprobanae* has been reported several times from outside of the *Pheretima* domain (Gates, 1970*c*). Its homeland is unknown but the species may come from southeast Asia since the numerical studies (see above) reveal that *taprobanae* has higher affinities with *iizukai* (from Japan) and *sempolensis* (from Java) than with representatives from New Guinea where it has been suggested that this taxon may have originated (Gates, 1972*a*).

MATERIAL EXAMINED. *Previously reported.* 1C Sri Lanka; BMNH 1904.10.5.165 (syntype of *taprobanae*). 6A Sri Lanka; BMNH 1972.1.6–11 (syntypes of *taprobanae*). 3C Northeast Madagascar; Hamburg v6935 (*taprobanae*: Michaelsen, 1907). 2C Sri Lanka; BMNH 1904.10.5.163–164 (*taprobanae*: Sims & Easton, 1972). 1C Brazil; Hamburg v9681 (*taprobanae* Michaelsen, 1927). *New records.* 15C, 8A Sri Lanka; BMNH 1904.10.5.1286–1296. 12C, 3A Queensland, Australia; BMNH 1972.11.67–73, 1973.14.272–279. 3C, 1A Suva point, Fiji; BMNH 1968.4.85–88. 1C Seychelles; BMNH 1977.21.4.

OTHER MATERIAL REPORTED. 1 specimen Sri Lanka (*taprobanae*: Michaelsen, 1903). 3 specimens Travencore, India (*taprobanae*: Aiyer, 1929). 6C Sri Lanka (*taprobanae*: Gates, 1945). 6 specimens Sri Lanka; Hamburg v4662 (syntypes of *pauli*) although this series is listed in the catalogue of the Hamburg Museum it could not be located during the preparation of this paper. 2C, 4A Brazil (*taprobanae pauli*: Moreira, 1903). Oahu, Hawaii (*taprobanae*: Gates, 1972) this material was identified by Dr G. E. Gates who included the record in his monograph on Burmese earthworms, although it was not noted as a new record (Gates, private communication).

Polypheretima grata (Cognetti, 1914)

Pheretima (*Parapheretima*) *grata* Cognetti, 1914 : 362; Ude, 1932 : 164.
Metapheretima grata: Sims & Easton, 1972 : 180, 233.

DIAGNOSIS. *Polypheretima* with male pores within copulatory pouches; spermathecal pores in furrows 5/6/7. Holandric. Stalked glands discharge into copulatory pouches and through papillae associated with spermathecal pores.

DESCRIPTION. *External characters.* Length 110–140 mm, diameter *c.* 4 mm. 83–100 segments. Clitellum *xiv–xvi*. First dorsal pore 13/14. Setae, *c.* 53 on *vii*, *c.* 68 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores on squat conical penes within copulatory pouches *c.* 0·30 body circumference apart. Female pore single. Spermathecal pores paired, intersegmental in 5/6/7, *c.* 0·50 body circumference apart.

Genital markings (Fig. 17c), small, simple papillae in paired clusters of up to 6, median to the spermathecal pores, postsetal on *vi*.
Internal characters. Septa 5/6–9/10 membranous, 10/11–13/14 thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs paired, extending to the dorsal line in *x* and *xi*, seminal vesicles in *xi* and *xii*, extending to the lateral line, those of *xi* enclosed in the testes sacs. Pseudoseminal vesicles large, *xiii*. Copulatory pouches large, well developed occupying the coelom. Male pores on squat conical penes. Up to 12 stalked glands discharge through small papillae with the copulatory pouches. Spermathecae (Fig. 14m) paired in *vi* and *vii*.

Stalked glands discharge through the genital markings on *vi* and into the copulatory pouches.

DISTRIBUTION. New Guinea.

REMARKS. The results of the numerical investigations (see above) could be interpreted as indicating that this species is closely allied to the *bifaria* species-group. If this is so then the copulatory pouches would have evolved independently of their development of other species of *Polypheretima* (*polytheca*, *patae* and *badia* species-groups).

MATERIAL EXAMINED. *Previously reported.* 2C Sepik river, Papua New Guinea (Cognetti also provided the following co-ordinates 4° 4′ 18″ S, 140° 7′ 15″ E. These lie a considerable distance from the Sepik river but it has not been possible to establish which data are correct); Leiden 1819 (syntypes of *grata*). 8C Sepik river, Papua New Guinea; Berlin 6466, 6467 (*grata*: Ude, 1932). *New record.* 1C Mt Wilhelmina, West Irian; Bogor Ann 065.

Polypheretima voeltzkowi (Michaelsen, 1907)

Pheretima voeltzkowi Michaelsen, 1907 : 45.
Metapheretima voeltzkowi: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with simple male pores; paired spermathecal pores on the postsetal region of *v*. Holandric.

DESCRIPTION. *External characters.* Length 40–68 mm, diameter 2·5–3·5 mm. 85–88 segments. Clitellum *xiv–xvi*. First dorsal pores 12/13. Setae, 55–60 on *vii*, 50–70 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores simple on large circular porophores *c.* 0·30 body circumference apart. Female pores paired. Spermathecal pores paired, segmental on the postsetal region of *v*, close to the intersegmental furrow, *c.* 0·66 body circumference apart.

Genital markings (Fig. 17b) simple, paired, postsetal on *xvii*, pre- and postsetal on *xviii*, median to the male pores.

Internal characters. Septa 5/6/7 thickened, 7/8–13/14 membranous. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Holandric, testes sacs paired, extending to the dorsal line in *x* and *xi*, seminal vesicles slim, extending to the dorsal line in *xi* and *xii*. Spermathecae (Fig. 14n) paired in *v*, occasionally absent.

DISTRIBUTION. Comoro Islands.

REMARKS. *P. voeltzkowi* is known only from the type series. Michaelsen (1907) recorded that the spermathecal pores are intersegmental in furrow 5/6 but re-examination of the type series revealed that they are on the postsetal portion of segment *v* close to the intersegmental furrow.

The Comoro Islands are outside of the presently accepted range of *Polypheretima* and indeed of the *Pheretima* domain. Numerical studies (see above) revealed that this species has high affinities with the Papuan representatives of the *P. bifaria* species-group and it is possible that the occurrence of *voeltzkowi* in the Comoro Islands is the result of accidental introduction by man.

MATERIAL EXAMINED. 3C Great Comoro, Comoro Islands; Hamburg v6936 (syntypes of *voeltzkowi*). 5C Data as above; Berlin 4946 (syntypes of *voeltzkowi*).

Polypheretima polytheca species-group

DIAGNOSIS. Holandric species of *Polypheretima* with male pores within copulatory pouches which lack stalked glands discharging into them.

DISTRIBUTION. Indochina, Malaya, Borneo, Western Indonesia.

SPECIES INCLUDED. *annamensis*, *aringeana*, *elongata* species-complex (*elongata*, *everetti*, *kinabaluensis*, *phacellotheca*, *stelleri*), *koyana*, *lesonea*, *pentacystis*, *polytheca*, *renschi*.

REMARKS. With the exception of *P. grata* all the holandric species of *Polypheretima* with specialized male pores are included in this species-group. *P. grata* may be distinguished by the possession of

Table 7 Marker characters of the members of the *Polypheretima polytheca* species-group

Species	Spermathecal furrows	Number of spermathecae per battery[1]	Separation of spermathecal batteries	Indigenous distribution
pentacystis	4/5/6/7/8/9	1	0·62	? Madagascar ? Seychelles
polytheca	5/6/7/8/9	6–10	0·28	Malaya
koyana	5/6/7/8/9	up to 9	0·20	Borneo
lesonea	5/6/7/8/9 or 6/7/8/9	1(5/6/7), 1–2 (7/8), 8–10(8/9)	0·25	Sumatra
elongata species-complex	5/6, 5/6/7 or 6/7	1–28	0·25	Sangihe, Kepulaud Taulaud, Celebes, Buru, Balabac Is., Borneo, ? Madura, East Java, Bali, Lombok, Sumbawa, Komodo, Gt Bastard Is.
aringeana[2]	5/6/7	7–10	0·50	Malaya
annamensis	6/7	1	0·20	Vietnam
renschi	7/8/9	1	? 0·25	Flores

[1] Species with paired spermathecae are coded as 1.
[2] *aringeana* may also be recognized by the form of its genital markings (see Figs 4e and 21b).

stalked glands discharging into the copulatory pouches and the small, numerous genital markings associated with the spermathecal pores.

Marker characters of the species included in the *polytheca* species-group are given in Table 7.

Polypheretima pentacystis (Rosa, 1891)

Perichaeta pentacystis Rosa, 1891 : 400; Beddard, 1895 : 422.
Amynthas pentacystis: Michaelsen, 1899 : 95; Beddard, 1900*a* : 614.
Pheretima pentacystis: Michaelsen, 1900 : 293.
Metapheretima pentacystis: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with male pores in copulatory pouches; paired spermathecal pores about three fifths of the body circumference apart in furrows 4/5/6/7/8/9. Holandric.

DESCRIPTION. *External characters.* Length 110–124 mm, diameter 5–6 mm. 82–113 segments. Clitellum *xiv–xvi.* First dorsal pore 13/14. Setae, 65–75 on *vii*, 80–86 on *xx*, setal ring regular with ventral gaps ($aa = 2ab = 2yz = 2zz$).

Male pores on squat conical penes within copulatory pouches *c.* 0·27 body circumference apart. Female pores paired. Spermathecal pores small, paired, intersegmental in 4/5/6/7/8/9, more widely separated anteriorly than posteriorly, *c.* 0·82 body circumference apart at 4/5, *c.* 0·62 body circumference apart at 8/9.

Genital markings (Fig. 21a) large, simple, paired, presetal on *viii*, *xvii* and *xix* slightly median to the line of the male pores.

Internal characters. Septa 5/6–7/8 thickened, 8/9 membranous, 9/10–12/13 thickened. Intestine begins in *xiv*. Lateral hearts in *x–xiii.*

Holandric, testes sacs paired in *x* and *xi* but linked dorsally by a narrow connection, seminal vesicles large, reaching the dorsal line in *xi* and *xii*. Copulatory pouches extending into the coelom. Spermathecae (Fig. 15a) paired in *v–ix*.

DISTRIBUTION. Seychelles, Madagascar.

REMARKS. The only records of *pentacystis*, the Seychelles and Madagascar, are from outside of the classical domain of the *Pheretima* group of genera. Presumably the species has been introduced into these islands by the agency of man. It is interesting to note that the variations in sizes and distributions of the spermathecal batteries among the other species of the *polytheca* species-group are clinal and if these trends were to be projected southwestwards from the range of the group, a form with five thecal segments and paired spermathecae would be expected to occur in the Seychelles–Madagascar area. At present, there are no explanations available to provide a mechanism for the dispersal of the *polytheca* species-group into this region.

Due to the extreme dorsal situation of the spermathecal pores in *pentacystis*, during copulation torsion of the anterior portion of the body may be necessary by both partners so as to apply the ventral region possessing the male pores to the region of the spermathecal pores. Possibly this behavioural requirement may act as a barrier preventing successful copulation between *pentacystis* and its siblings in the *polytheca* species-group.

MATERIAL EXAMINED. 1C Mahe Island, Seychelles; Wein 3996 (holotype of *pentacystis*). 1C Nossibe, Madagascar; Hamburg v5113 (*pentacystis*: Michaelsen, 1899).

Polypheretima polytheca (Beddard, 1900)

Amynthas polythecus Beddard, 1900*b* : 897.
Pheretima polytheca: Stephenson, 1932 : 229; (=*minuta*) Gates, 1935 : 89.
Pheretima (*Polypheretima*) *polytheca*: Michaelsen, 1934*b* : 16.
Metapheretima polytheca: Sims & Easton, 1972 : 181, 233. [non *Pheretima polytheca aruensis* Michaelsen, 1910*a* : 252. *Pheretima* (*Polypheretima*) *polytheca aruensis*: Michaelsen, 1934*b* : 16, 29. *Metapheretima polytheca aruensis*: Sims & Easton, 1972 : 233 (= ? *Polypheretima bifaria*).]
Amynthas minutus Beddard, 1900*b*: 906. [non *Pheretima minuta* Gates, 1929: 18 (=*Amynthas exiguus*).]
Pheretima minuta: Stephenson, 1932 : 222.
Pheretima (*Polypheretima*) *minuta*: Michaelsen, 1934*b* : 16.
Metapheretima minuta: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with male pores in shallow copulatory pouches about one quarter of the body circumference apart; numerous spermathecal pores in paired batteries about one third of the body circumference apart in furrows 5/6/7/8/9. Holandric.

DESCRIPTION. *External characters.* Length 44–50 mm, diameter 1·5–2 mm. 84–105 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, 45–50 on *vii*, 40–50 on *xx*, setal ring regular with dorsal and ventral gaps ($aa = 2ab = 2yz = zz$).

Male pores on large circular porophores within shallow copulatory pouches *c.* 0·24 body circumference apart. Female pore single. Spermathecal pores small, numerous in paired batteries of 6–10 pores intersegmental in 5/6/7/8/9 *c.* 0·28 body circumference apart.

Genital markings (Fig. 21b), simple paired, presetal on *vi* and *viii* slightly median to the spermathecal batteries, on *xvii*, *xix–xxi* slightly median to the line of the male pores.

Internal characters. Septa 5/6–7/8 thickened, 8/9/10 absent, 10/11–12/13 thickened. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Holandric, testes sacs large, paired in *x* and *xi*, extending to the dorsal line and in *xi* enclosing the lateral hearts and seminal vesicles, seminal vesicles large, extending to the dorsal line in *xi* and *xii*. Pseudoseminal vesicles well developed in *xiii*. Copulatory pouches shallow, confined to the body wall. Spermathecae (Fig. 15b) numerous, arranged in paired, batteries of 6–10 spermathecae in *vi–ix*.

DISTRIBUTION. Kelantan, Malaya.

REMARKS. The taxon *polytheca aruensis*, described by Michaelsen (1910) from material collected in the Aru Islands, is tentatively placed in the synonymy of *Polypheretima bifaria* mainly on the arrangement of genital markings.

MATERIAL EXAMINED. 1C Kelantan, Malaya; BMNH 1924.3.1.249 (holotype of *polytheca*). 1C Kelantan, Malaya; BMNH 1924.3.1.219 (holotype of *minuta*).

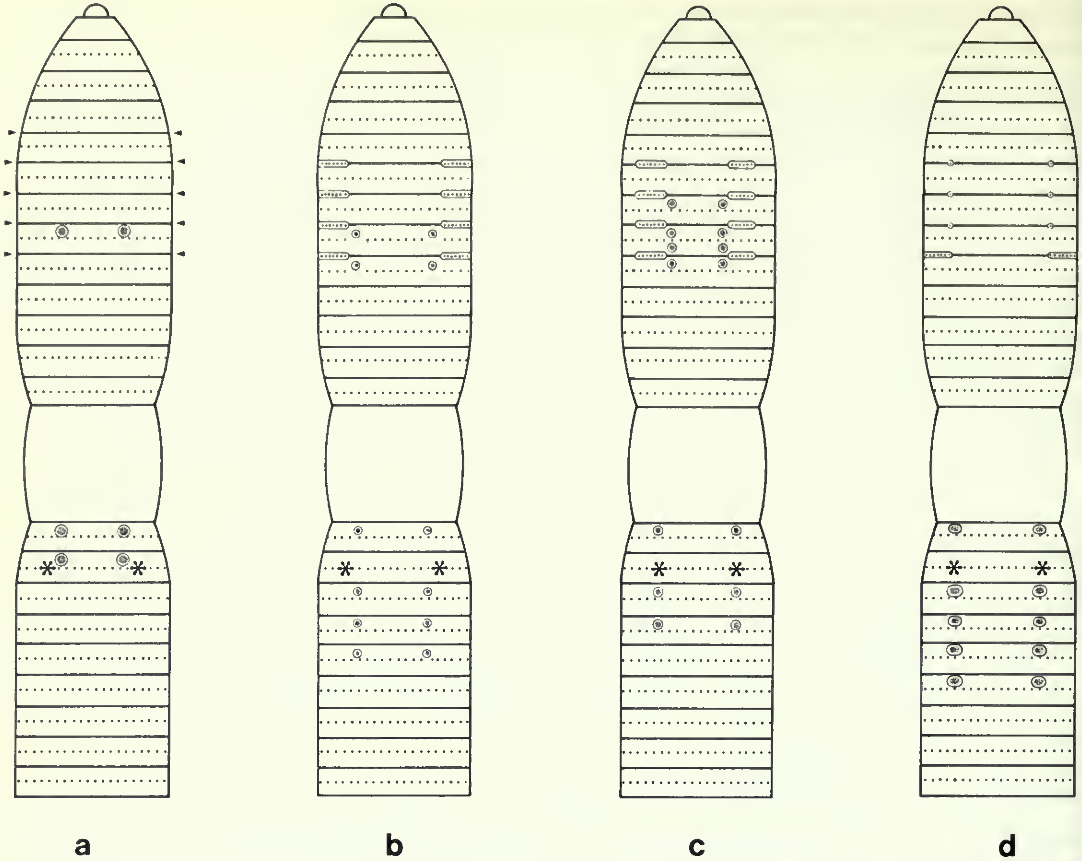

Fig. 21 Anterior ventral surface, diagnostic characters. (For ontogenetic variation of the male pores, see Fig. 3.) (a) *Polypheretima pentacystis*, arrows indicate furrows with dorsal spermathecal pores; (b) *P. polytheca*; (c) *P. koyana*; (d) *P. lesonea* sp. nov.

Polypheretima koyana (Michaelsen, 1934)

Pheretima (*Polypheretima*) *koyana* Michaelsen, 1934*b* : 29.
Metapheretima koyana: Sims & Easton, 1972 : 180, 233.

DIAGNOSIS. *Polypheretima* with male pores within large copulatory pouches about one fifth of the body circumference apart; numerous spermathecal pores in paired batteries about one fifth of the body circumference apart in furrows 5/6/7/8/9. Holandric.

DESCRIPTION. *External characters.* Length 125–230 mm, diameter 3·5–5 mm. 162–175 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, 40–45 on *vii* and *xx*, setal ring regular on preclitellar segments ($aa = ab = yz = zz$), and with dorsal and ventral gaps on postclitellar segments ($aa = 1{\cdot}5ab = 1{\cdot}5yz = zz$).

Male pores on squat conical penes within crescentic copulatory pouches *c.* 0·17 body circumference apart. Female pore single or paired. Spermathecal pores small, numerous, in paired batteries of up to 9 pores, intersegmental in 5/6/7/8/9, *c.* 0·20 body circumference apart.

Genital markings (Fig. 21c) simple, paired, presetal on *vii–ix*, and postsetal on *viii*, slightly median to the spermathecal batteries, presetal on *xvii*, *xix–xx*, slightly median to the male pores. *Internal characters.* Septa 5/6–7/8 thickened, 8/9/10 absent, 10/11–13/14 thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs small, paired, ventral in *x* and *xi*, seminal vesicles large, reaching the dorsal line in *xi* and *xii*. Pseudoseminal vesicles in *xiii*. Copulatory pouches large, extending into

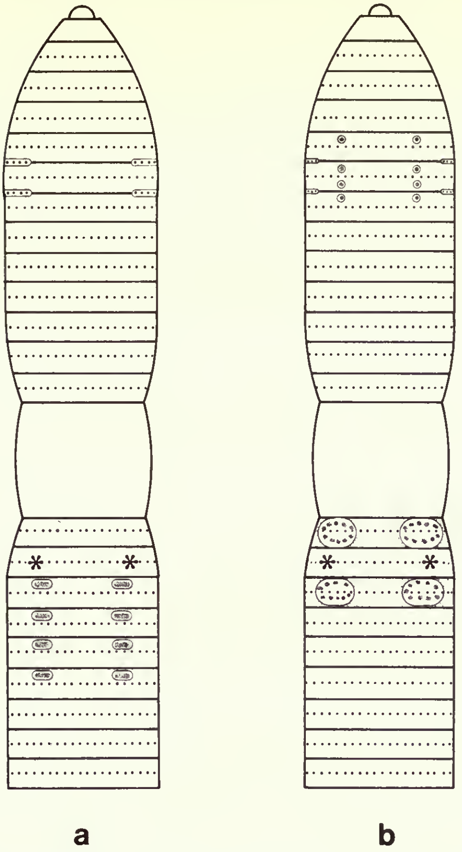

Fig. 22 Anterior ventral surface, diagnostic characters. (For ontogenetic variation of the male pores see Fig. 3.) (a) *Polypheretima elongata*; (b) *P. aringeana.*

the coelom. Spermathecae (Fig. 15c), numerous, arranged in paired batteries of up to 9 spermathecae in *vi–ix.*

Distribution. Mt Dulit, Sarawak.

Material examined. 2C, 6A Mt Dulit, Sarawak; BMNH 1933.10.6.21–25 (syntypes of *koyana*). 3C, 2A Data as above; Hamburg v11954, v11952 (syntypes of *koyana*).

Polypheretima lesonea sp. nov.

Diagnosis. *Polypheretima* with male pores within copulatory pouches about one third of the body circumference apart; paired spermathecal pores in furrows 6/7/8 and often 5/6, numerous, spermathecal pores in paired batteries in 8/9. Holandric.

Description. *External characters.* Length 73–88 mm, diameter 2–3 mm. 112–131 segments. Clitellum *xiv–xvi.* First dorsal pore 11/12. Setae, 34–40 on *vii*, 30–36 on *xx*, setal ring regular with ventral gaps on preclitellar segments ($aa=2ab=2yz=2zz$), and with dorsal and ventral gaps on postclitellar segments ($aa=2ab=2yz=zz$).

Male pores on squat conical penes within copulatory pouches, *c.* 0·33 body circumference apart. Female pore single. Spermathecal pores small, intersegmental, in 6/7/8/9 and occasionally 5/6 also, pores paired in 5/6/7/8, *c.* 0·42 body circumference apart and in paired batteries of 8–10 pores in 8/9 where the ventralmost pores are *c.* 0·42 body circumference apart and the dorsalmost are close to the dorsal line, additional spermathecal pores in 7/8 occasionally.

Genital markings (Fig. 21d) paired, presetal on *xix–xxii* and occasionally *xvii* in line with the male pores.
Internal characters. Septa 5/6–7/8 thickened, 8/9 absent, 9/10 membranous, 10/11–12/13 thickened. Intestine begins in *xvi*. Lateral hearts in *x–xiii*.

Holandric, testes sacs large, paired, reaching the dorsal line in *x* and *xi*, enclosing the lateral hearts and, in *xi*, the seminal vesicles, seminal vesicles small in *xi*, large, reaching the dorsal line in *xii*. Coelomic pouches small, invading the coelom. Spermathecae (Fig. 15d) in *vii–ix* and occasionally *vi*, paired in *vi–viii*, in paired batteries of 8–10 spermathecae in *ix*, additional spermathecae in *viii* occasionally.

DISTRIBUTION. Sumatra.

REMARKS. All of the syntypes of this species have three thecal segments (*vii–ix*) and are bithecal in the first two and polythecal in the last segment. The single individual from Maurarupit has an additional pair of spermathecae in *vi* and is polythecal in *viii* (2 spermathecae in each battery).

MATERIAL EXAMINED. 8C Flat plain mostly covered with sedge grass and scrub trees and with few cultivations or villages, soil damp, loamy, shallow, Sungaikolong, Central Sumatra, 1° 07′ S, 101° 48′ E, altitude *c.* 50 m, *coll* G Lincoln 28 May 1973 British University Dragon Expedition; BMNH 1975.7.3–12 (syntypes of *lesonea*). 1C Flat ground beside river, moist black soil and mud, c 5 miles south of Maurarupit, beside road to Lapat, central Sumatra, 2° 45′ S, 102° 54′ E, altitude *c.* 160 m, *coll* G Lincoln 5 Jun 1973 British University Dragon Expedition; BMNH 1975.7.2.

Polypheretima elongata species-complex

Metapheretima elongata species-complex Sims & Easton, 1972 : 252; Easton, 1976 : 38.

DIAGNOSIS. *Polypheretima* with male pores in shallow copulatory pouches lacking stalked glands; numerous spermathecal pores in paired batteries in furrows 5/6 and/or 6/7. Holandric, postclitellar genital markings one pair per segment, simple presetal near to the line of the male pores.

DESCRIPTION. *External characters.* Length 40–360 mm, diameter 1·5–10 mm. 100–220 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae 20–130 on *vii*, 36–86 on *xx*, occasionally setae *a* and *b* enlarged, setal ring regular with ventral gaps ($aa = 1{\cdot}5ab = 1{\cdot}5yz = 1{\cdot}5zz$).

Male pores on squat penes within shallow copulatory pouches *c.* 0·25 body circumference apart. Female pore single. Spermathecal pores small, numerous arranged in paired ventrolateral batteries, of up to 28 pores, intersegmental in 5/6 and/or 6/7, occasionally absent.

Genital markings (Fig. 22a) simple, large, paired presetal on *xix* and successive segments in line with or slightly median to the male pores, occasionally on *vi*, *vii* and *xvii*.
Internal characters. Septa 4/5–7/8 thickened, 8/9 membranous, 9/10 absent, 10/11–13/14 thickened. Intestine begins in *xv*. Lateral hearts in *x–xii* and usually *xiii*.

Holandric, testes sacs large, paired, extending to the dorsal line in *x* and *xi*, seminal vesicles paired in *xi* and *xii*, the anterior pair enclosed in the testes sacs. Pseudoseminal vesicles in *xiii* and *xiv*. Copulatory pouches shallow, confined to the body wall. Spermathecae (Fig. 15e) numerous in paired batteries of up to 28 spermathecae in *vi* and/or *vii*, occasionally absent.

DISTRIBUTION. *Indigenous records.* Kepulaud Taulaud; Sangihe; Celebes; Buru; Balabac Island, Palawan; Borneo; ? Madura; east Java; Bali; Lombok; Sambawa; Komoda; Gt Bastard Island, Flores.

Four of the five species included in this species-complex are known only from the indigenous range. The fifth, *elongata*, has been introduced into may parts of the world.

REMARKS. The species *elongata*, *everetti*, *kinabaluensis*, *phacellotheca* and *stelleri* form a single species-complex. They may be distinguished from one another by comparisons of the number of setae on *vii* and the size of the spermathecal batteries (Fig. 23). The spermathecal index may be calculated by substituting the mean size of the anterior and posterior spermathecal batteries of an individual for *a* and *b* in the formula $x = \sqrt{(a^2 + b^2)}$. The four species, *everetti*, *phacellotheca*,

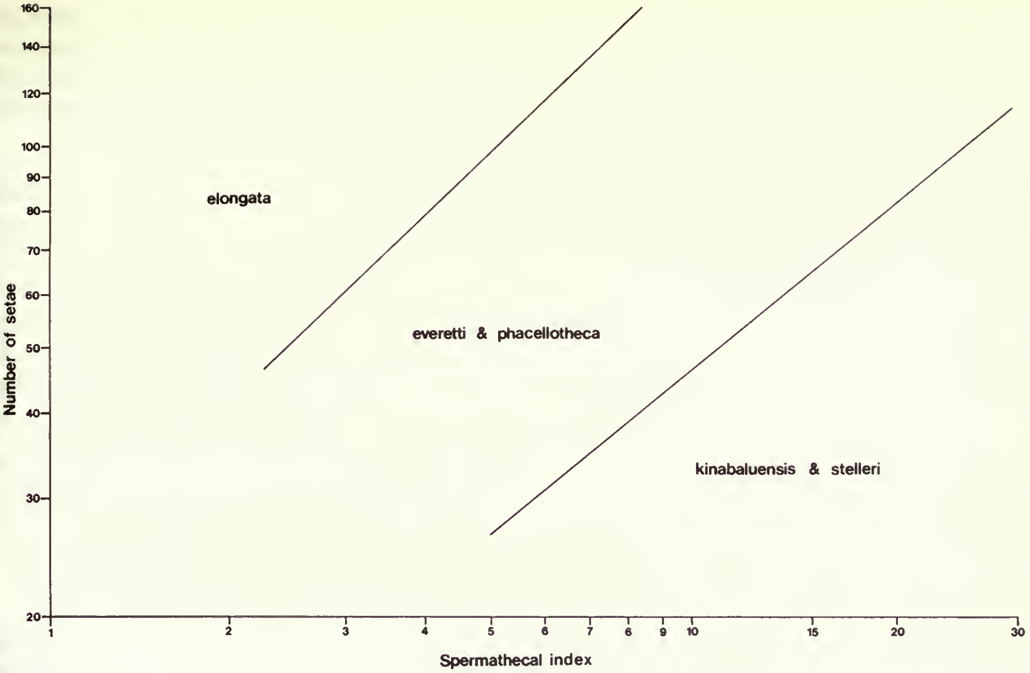

Fig. 23 *Polypheretima elongata* species-complex: correlation between the number of setae on segment *vii* and the spermathecal index, $\sqrt{(a^2+b^2)}$. (a and b are the mean number of spermathecae in a battery in furrows 5/6 and 6/7 respectively.)

stelleri and *kinabaluensis*, need additional characters to be assessed for differentiation. In the first pair *everetti* has spermathecal pores in furrows 5/6 and 6/7 while *phacellotheca* has spermathecae in furrow 5/6 only; in the second *stelleri* has numerous setae on *vii* (up to 130) while *kinabaluensis* has few setae (less than 40). Full details of the variation in the setal and spermathecal systems of the members of the *elongata* species-complex are given by Easton (1976).

Polypheretima elongata (Perrier, 1872)

Perichaeta elongata Perrier, 1872 : 124.
Metapheretima elongata: Easton, 1976 : 40.
Perichaeta biserialis Perrier, 1875 : 1044.
Perichaeta acystis Beddard, 1895: 423.
(For full synonomy see Easton, 1976.)

DIAGNOSIS. *P. elongata* species-complex with numerous setae (usually about 80 on *vii* in clitellate specimens but up to 130 in large individuals); small spermathecal batteries (rarely more than 3 spermathecae in each battery) in furrows 5/6/7 or 5/6 or 6/7 only or absent. Spermathecal batteries usually present in about 50% of the clitellate portion of indigenous populations to only 15% of the clitellate portion of introduced populations (Easton, 1976).

DISTRIBUTION. *Indigenous records.* ? Madura; east Java; Bali; Lombok; Sumbawa; Komodo; ? Gt Bastard Island, Flores; ? southeast Celebes.
Introduced records. South and central America (type locality, Peru), Madagascar, Comoros, Sri Lanka, India, Pakistan, Bangladesh, Burma, Andaman Islands, Thailand, Malaya, Sumatra, west and central Java, Kepulaud Taulaud, Philippines, Taiwan, Kei Islands, Australia, Papua New Guinea, New Britain (new record), New Caledonia, Caroline Islands, Ryukyu Islands, Hawaii, Tahiti, West Indies, Africa. (See Gates, 1972*a* : 182 for further details.)

Remarks. Individuals of this species often lack spermathecae. Athecate individuals are especially numerous in introduced populations in which, presumably, specimens without spermathecae reproduced parthenogenetically (Gates, 1972*a* : 182). The incidence of thecate individuals can be used to establish the indigenous range of the species by analysing the composition of long series (Easton, 1976).

Polypheretima everetti (Beddard & Fedarb, 1895)

Perichaeta everetti Beddard & Fedarb, 1895 : 69.
Perichaeta papillata Beddard & Fedarb, 1895 : 71.
Perichaeta sarawacensis Beddard & Fedarb, 1895: 71.
Perichaeta barami Michaelsen, 1896 : 203.
Amynthas stelleri seriatus Michaelsen, 1899 : 44.
Amynthas stelleri klabatensis Michaelsen, 1899 : 46.
Amynthas stelleri bonensis Michaelsen, 1899 : 45 [non *Pheretima* (*Pheretima*) *stelleri bonensis*: Michaelsen, 1934*a* : 108 (=*P. phacellotheca*)].
Pheretima stelleri koroensis Michaelsen, 1910*b* : 109.
Pheretima stelleri mahakkami Michaelsen, 1922 : 25.
Pheretima (*Pheretima*) *beranensis* Michaelsen, 1928*a* : 23.
Pheretima (*Polypheretima*) *beranensis tinjarana* Michaelsen, 1934*b* : 25.
Pheretima (*Pheretima*) *baritoensis* Michaelsen, 1932 : 9.
Metapheretima everetti: Easton, 1976 : 41.
(For full synonomy see Easton, 1976.)

Diagnosis. *P. elongata* species complex with numerous setae (up to 130 on *vii* in large individuals); intermediate sized spermathecal batteries (usually 6–12 spermathecae in each battery of large individuals) in furrows 5/6/7. Spermathecal batteries present in aclitellate as well as clitellate individuals (Easton, 1976).

Distribution. Balabac Island, Palawan (type locality); north and west Celebes; Borneo (up to 2400 m); Lombok (*c*. 350–450 m only).

This species is unknown outside its indigenous range.

Remarks. On Lombok this species has been recorded only from localities at altitudes between 350 and 450 m. Samples from lower altitudes contained the species *elongata* which is rare at higher altitudes. No samples of earthworms are known from above 450 m on Lombok. Although altitudes would appear to be the primary factor governing the distribution of *everetti* (and *elongata*), it should be noted that, on Lombok, the samples of *everetti* were from natural woodland (those of *elongata* being from cultivated land). All the records of *everetti* (also *stelleri* and *phacellotheca*) from Celebes are from the northern and western region, an area of forest. On Mt Kinabalu, Borneo, the species *everetti* occurs at altitudes up to 2400 m, being sympatric from 2100 m with the high altitude species *kinabaluensis*. Although on both Lombok and Mt Kinabalu *everetti* is sympatric with other members of the *elongata* species-complex, there is no indication of hybridization among them.

Beddard & Fedarb (1895) reported that the type locality of *Perichaeta everetti* is Mt Kinabalu, Sabah but Easton (1976) redesignated Balabac Island, Palawan as the type locality under Recommendation 72E of the International Code of Zoological Nomenclature.

Polypheretima kinabaluensis (Beddard & Fedarb, 1895)

Perichaeta kinabaluensis Beddard & Fedarb, 1895 : 71.
Metapheretima kinabaluensis: Easton, 1976 : 41.
(For full synonomy see Easton, 1976.)

Diagnosis. *P. elongata* species-complex with few setae (less than 40 on *vii*); intermediate sized spermathecal batteries (usually 6–12 spermathecae in each battery of large individuals) in furrows 5/6/7. Spermathecal batteries present in aclitellate as well as clitellate individuals (Easton, 1976).

Distribution. Mt Kinabalu, Sabah. 2100–2750 m (type locality Tamburgare, 2350 m).

This species has not been recorded outside its indigenous range.

REMARKS. This species is known only from high altitudes on Mt Kinabalu where there is a specialized montane fauna and flora. Although samples collected on Mt Kinabalu at 2100 and 2400 m contained both *everetti* and *kinabaluensis*, there is no indication of hybridization.

Polypheretima phacellotheca (Michaelsen, 1899)

Amynthas phakellotheca (sic) Michaelsen, 1899 : 47.
Metapheretima phacellotheca: Easton, 1976 : 44.
(For full synonomy see Easton, 1976.)

DIAGNOSIS. *P. elongata* species-complex with numerous setae (up to 80 on *vii* in large individuals); large spermathecal batteries (9–12 spermathecae in each battery of large individuals) in furrow 5/6 only. Spermathecal batteries present in aclitellate as well as clitellate individuals (Easton, 1976).

DISTRIBUTION. Northeast Celebes (type locality; Mt Masarang, near Tomohon), Buru.

REMARKS. This species is the only member of the *elongata* species-complex known from Buru which is the most easterly indigenous record of the complex. Morphologically it closely resembles *stelleri* from which it may be distinguished by the restriction of spermathecal batteries to furrow 5/6.

Polypheretima stelleri (Michaelsen, 1891)

Perichaeta stelleri Michaelsen, 1891 : 39.
Amynthas stelleri annectens Michaelsen, 1899 : 42.
Metapheretima stelleri: Easton, 1976 : 44.
(For full synonomy see Easton, 1976.)

DIAGNOSIS. *P. elongata* species-complex with numerous setae (up to 130 on *vii* in large individuals); very large spermathecal batteries (up to 28 spermathecae in each battery of large individuals) in furrows 5/6/7. Spermathecal batteries present in aclitellate as well as clitellate individuals (Easton, 1976).

DISTRIBUTION. Sangihe (type locality), Kepulaud Taulaud, Celebes (Bone valley and Matinang range).

This species has not been encountered outside its indigenous range.

REMARKS. In Celebes *stelleri* has been recorded from Bone valley (*c.* 400 m) and the Matinang range (*c.* 1500 m) together with *everetti.*

Polypheretima aringeana (Beddard, 1900)

Amynthas aringeanus Beddard, 1900*b* : 899.
Pheretima argineana: Stephenson, 1932 : 203.
Pheretima (*Polypheretima*) *aringeana*: Michaelsen, 1934*b* : 16.
Metapheretima aringeana: Sims & Easton, 1972 : 180, 233.

DIAGNOSIS. *Polypheretima* with male pores in shallow copulatory pouches lacking stalked glands; numerous spermathecal pores arranged in paired batteries, in furrows 5/6/7. Holandric, postclitellar genital markings, 1 pair per segment, central portion of each marking differentiated into several small pigmented areas (Fig. 4e, 22b).

DESCRIPTION. *External characters.* Length 60–200 mm, diameter 3–5 mm. 100–150 segments. Clitellum *xiv–xvi.* First dorsal pore 12/13. Setae, 60–70 on *vii*, and *xx*, setal ring slightly crowded ventrally with ventral gaps on preclitellar segments ($aa = 1{\cdot}5ab = 2yz = 2zz$), evenly spaced on postclitellar segments ($aa = ab = yz = zz$).

Male pores on large conical penes within copulatory pouches *c.* 0·27 body circumference apart. Female pore single. Spermathecal pores numerous, arranged in paired, lateral batteries of 7–10 pores, intersegmental in 5/6/7, *c.* 0·50 body circumference apart.

Genital markings (Fig. 22b) simple paired presetal on *v–vii* and postsetal on *v* and *vi*, slightly median to the spermathecal batteries; large paired markings differentiated central areas, occupying the whole length of the segment, in line with the male pores on *xvii* and *xix*.
Internal characters. Septa 4/5–7/8 thickened, 8/9/10 absent, 10/11–12/13 thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs annular in *x* and *xi*, enclosing the lateral hearts and, in *xi*, the seminal vesicles, seminal vesicles small in *xi*, large in *xii*. Pseudoseminal vesicles large in *xiii*. Copulatory pouches shallow, confined to the body wall. Spermathecae (Fig. 15f), numerous, arranged in paired batteries of 7–10 spermathecae in *vi* and *vii*.

DISTRIBUTION. Malaya.

MATERIAL EXAMINED. *Previously reported.* 3C, 4A Kelantan, Malaya; BMNH 1904.10.5.1000–1001, 1924.3.1.232–234 (syntypes of *aringeana*), other specimens from this series are deposited at Cambridge, England, they were not examined.
New record. 11C, 6A, Kelantan, Malaya; BMNH 1972.12.9–11, 1977.9.1–9.

Polypheretima annamensis (Stephenson, 1931)

Pheretima annamensis Stephenson, 1931 : 60.
Metapheretima annamensis: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with male pores in copulatory pouches; paired spermathecal pores about one fifth of the body circumference apart in furrow 6/7 only. Holandric.

DESCRIPTION. *External characters.* Length 84–87 mm – both of the specimens on which this description is based are immature, adult individuals may be expected to be considerably larger – diameter *c.* 6 mm. *c.* 177 segments. Clitellum *xiv–xvi*. First dorsal pore 11/12. Setae, 82–86 on *vii*, *c.* 94 on *xx*, setal ring regular on preclitellar segments ($aa = ab = yz = zz$), with ventral gaps on postclitellar ($aa = 1{\cdot}5ab = 1{\cdot}5yz = 1{\cdot}5zz$).

Male pores on squat penes within large copulatory pouches *c.* 0·23 body circumference apart. Female pores not detected. Spermathecal pores paired, intersegmental in 6/7, *c.* 0·20 body circumference apart.

Genital markings absent.
Internal characters. Septa 5/6–7/8 thickened, 8/9/10 absent, 10/11–13–14 thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs of *x* annular, those of *xi* small, paired lateral, seminal vesicles large in *xi* and *xii*, reaching the dorsal line. Copulatory pouches shallow, confined to the body wall. Spermathecae (Fig. 15g) paired in *vii*.

DISTRIBUTION. South Vietnam.

MATERIAL EXAMINED. 1C, 1A Lang Bian Peaks, South Vietnam; BMNH 1930.2.7.10–11 (syntypes of *annamensis*).

Polypheretima renschi (Ude, 1932)

Pheretima (*Pheretima*) *renschi* Ude, 1932 : 141.
Metapheretima renschi: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with male pores in copulatory pouches; paired spermathecal pores in furrows 7/8/9. Holandric.

DESCRIPTION. *External characters.* Length 220–250 mm, diameter 8–12 mm. *C.* 160 segments. Clitellum *xiv–xvi*. Position of first dorsal pore not recorded. Setae, *c.* 72 on *vii*, *c.* 80 on *xiii*, small, widely spaced.

Male pores within copulatory pouches separated by 18 setae (estimated to be *c.* 0·25 body circumference apart). Female pores not recorded. Spermathecal pores paired, intersegmental in 7/8/9, separated by 18 setae (estimated to be *c.* 0·25 body circumference apart).

Genital markings absent.

Internal characters. Septa 7/8 membranous, 8/9 and probably 9/10 absent, 10/11–14/15 thickened. Intestine begins in *xv*. Disposition of lateral hearts not recorded.

Holandric, testes sacs paired, median in *x* and *xi*, seminal vesicles in *xi* and *xii*. Copulatory pouches confined to body wall, penes conical. Spermathecal, paired in *viii* and *ix*, ampulla sac shaped with a distinct, long, narrow duct. Diverticula three times as long as main duct with a bean shaped ampulla.

Description after Ude (1932).

DISTRIBUTION. Flores.

RECORDS. 2 specimens, west Flores (syntypes of *renschi*).

Polypheretima badia species-group

DIAGNOSIS. *Polypheretima* with a pair of simple presetal genital markings on each of several postclitellar segments. Metandric.

DISTRIBUTION. Lombok, Flores.

SPECIES INCLUDED. *badia*, *elberti*, *kellneri*, ? *sibogae*, *swelaensis*.

REMARKS. The metandric species of *Polypheretima* form two species-groups. Those from Papua are placed in the *patae* species-group, while those from the Lesser Sunda Islands comprise the *badia* species-group. The numerical investigation carried out during this revision indicate that these two groups are closely related in spite of their separate distributions. The oligochaete fauna of the area between these two species-groups is poorly known and it is uncertain whether the two groups are the end members of a continuous group of metandric species.

One species, *sibogae*, can be only tentatively assigned to the *badia*-group since data regarding its anterior male organs are deficient but the high affinities of this species with the other members of the species-group (see numerical studies) indicate that it is probably metandric.

The relationships among the taxa assigned to this group have not been studied in detail. Two of the species, *badia* and *swelaensis*, are certainly closely allied and possibly conspecific since the regions of their male pores are modified in the form of slight ridges which extend from *xvii* to *xix*.

Marker characters of the species assigned to the *badia* species-group are given in Table 8.

Table 8 Marker characters of the members of the *Polypheretima badia* species-group

Species	Spermathecal furrows	Separation of spermathecal pores	Setal number on *vii* (for segmental volume of *c.* 50 mm³)	Distribution
kellneri	4/5/6/7/8/9	0·50	30–40	Lombok
sibogae	4/5/6/7/8/9	0·40 (polythecal)	*c.* 200	Lombok
badia	4/5/6/7/8/9, 5/6/7/8/9 or ? 6/7/8/9	0·33	30–40	Flores ? Lombok
elberti	5/6/7/8/9	0·45	30–40	Lombok
swelaensis	5/6/7/8	0·37	60–80	Lombok

Polypheretima kellneri (Ude, 1932)

Pheretima (*Metapheretima*) *kellneri* Ude, 1932 : 177.
Metapheretima kellneri: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with paired spermathecal pores about one half of the body circumference apart in furrows 4/5/6/7/8/9. Metandric.

DESCRIPTION. *External characters.* Length *c.* 180 mm, diameter *c.* 4 mm. Segment number not recorded. Clitellum *xiv–xvi*. Setae, *c.* 42 on *viii*, c. 60 on *ix*, *c.* 62 on *xvi*, *c.* 65 on *xxi*, setal ring regular (*aa* = *ab* = *yz* = *zz*).

Male pores simple, *c.* 0·40 body circumference apart. Female pore single. Spermathecal pores paired, intersegmental in 4/5/6/7/8/9, *c.* 0·50 body circumference apart.

Genital markings absent.

Internal characters. Anterior septa present and those anterior to 13/14 slightly thickened. Intestine begins in *xv*. Disposition of lateral hearts not recorded.

Metandric, testes sacs paired in *xi*, seminal vesicles large in *xii*. Spermathecae, paired in *v–ix*, ampulla sac shaped with a short, poorly differentiated duct, diverticular slightly longer than main portion and with a cylindrical end chamber.

Description after Ude (1932).

DISTRIBUTION. Lombok.

REMARKS. *P. kellneri* is known only from the type series whose members lacked genital markings. It is probable that when more (mature) material becomes available individuals will be found with genital markings resembling the markings of other members of the *badia* species-group.

RECORDS. Lombok (type(s) of *kellneri*). Ude (1932) recorded this material as being in the Berlin Museum but no record of it could be found during the preparation of this paper; Dr G. Hartwich, personal communication.

Polypheretima sibogae (Michaelsen, 1922)

Pheretima sibogae Michaelsen, 1922 : 23.
Pheretima (*Polypheretima*) *sibogae*: Michaelsen, 1934*b* : 16.
Ephemitra sibogae: Sims & Easton, 1972 : 180, 232.

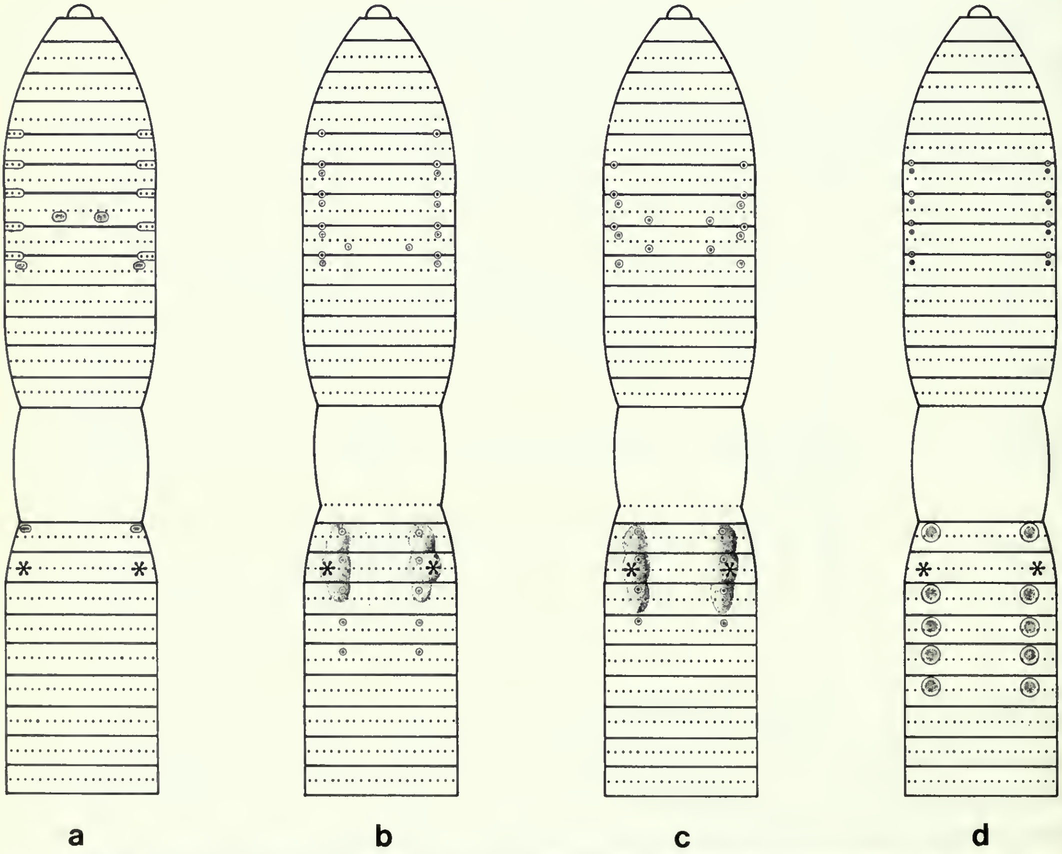

Fig. 24 Anterior ventral surface, diagnostic characters. (For ontogenetic variation of the male pores see Fig. 3.) (a) *Polypheretima sibogae*; (b) *P. badia*; (c) *P. swelaensis*; (d) *P. elberti*.

DIAGNOSIS. *Polypheretima* with numerous spermathecal pores arranged in paired batteries about two fifths of the body circumference apart in furrows 4/5/6/7/8/9. Meroandric. One pair of presetal genital markings on each of several postclitellar segments.

DESCRIPTION. *External characters.* Length *c.* 50 mm, diameter *c.* 3 mm. *C.* 73 segments. Clitellum *xiv–xvi.* First dorsal pore 12/13. Setae, *c.* 47 on *vii*, *c.* 58 on *xx*, setal ring regular with ventral gaps ($aa = 2ab = 2yz = 2zz$).

Male pores simple, *c.* 0·30 body circumference apart. Female pores paired. Spermathecal pores numerous, arranged in paired batteries of 5–11 pores, intersegmental in 4/5/6/7/8/9, *c.* 0·40 body circumference apart.

Genital markings (Fig. 24a), simple paired, presetal, slightly median to the spermathecal pores in *ix*, postsetal, close to the median line on *vii*, presetal, in line with the male pores on *xvii*. *Internal characters.* Anterior septa posterior to 5/6 present, unthickened. Beginning of the intestine not recognized. Disposition of the lateral hearts unknown.

Meroandric (proandric or metandric), testes sacs paired, no other details of the anterior male reproductive system known. Spermathecae (Fig. 15h) numerous in paired batteries of 5–11 spermathecae in *v–ix*.

DISTRIBUTION. Lombok.

REMARKS. *P. sibogae* is known only from the holotype which is poorly preserved. Due to its condition the position of the testes, whether it was proandric or metandric, cannot be established. The species is tentatively included in the *badia* species-group since its genital markings and distribution resemble those of other members of the group.

This species was included within the genus *Ephemitra* (= *Metapheretima* SS) by Sims & Easton (1972) but their decision was based on the assessment of the few characters observable from the holotype. In the present numerical studies *sibogae* has high affinities with the metandric species of *Polypheretima* from Lombok and Flores.

MATERIAL EXAMINED. 1C Lombok; Leiden 1823 (holotype of *sibogae*).

Polypheretima badia (Ude, 1932)

Pheretima (*Metapheretima*) *badia* (? part) Ude, 1932 : 171.
Metapheretima badia: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with paired spermathecal pores about one third of the body circumference apart in furrows 5/6/7/8/9 and often 4/5. Metandric. One pair of presetal genital markings on each of sevetal postclitellar segments.

DESCRIPTION. *External characters.* Length 85–160 mm, diameter 3–7mm. 68–105 segments. Clitellum *xiv–½xvi.* First dorsal pore 11/12 or 12/13. Setae 33–42 on *vii*, 50–70 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores simple, superficial or slightly invaginated, *c.* 0·33 body circumference apart. Female pores paired. Spermathecal pores paired, intersegmental in 4/5/6/7/8/9, anterior pair (? and next pair) often absent, *c.* 0·33 body circumference apart.

Genital markings (Fig. 24b) simple, paired, presetal on *vi–ix* slightly median to the spermathecal pores, postsetal on *viii* close to the median line, presetal on *xvii–xxiii* median to the male pores. Body wall of *xvii-xix* bearing male pores and genital markings elevated to form paired ridges. *Internal characters.* Anterior septa posterior to 5/6 present and membranous or slightly thickened. Intestine begins in *xv*. Lateral hearts in *x–xii.*

Metandric, testes sacs paired in *xi* with narrow dorsal processes, seminal vesicles in *xii*, reaching the dorsal line. Pseudoseminal vesicles in *xiv*. Spermathecae very similar to those of *swelaensis* (Fig. 15j) paired in *v–ix*, anterior pair (? and the next pair) often absent.

DISTRIBUTION. West Flores and (possibly) east Lombok.

REMARKS. *P. badia* was described originally from two series, one collected on Lombok and the other on Flores. The species is now known only from the four extant specimens of the series from

Flores since Easton (1976) found that the single extant specimen from Lombok was the polythecal, holandric species *Polypheretima everetti* (Beddard & Fedarb, 1895). None of these individuals have been dissected so it must be assumed that Ude had other material at his disposal when he described the internal anatomy.

The above description now differs somewhat from the original. In the original account of *badia* the spermathecal pores were reported as being in furrows 5/6/7/8/9 or 6/7/8/9. Of the specimens re-examined from Flores two have spermathecae opening into furrows 5/6/7/8/9 while the other two have spermathecae opening into furrows 4/5/6/7/8/9. It appears that the original description is unreliable, and it is therefore uncertain whether the species occurs on Lombok.

MATERIAL EXAMINED. 4C West Flores; Berlin 7213 (syntypes of *badia*).

Polypheretima elberti (Ude, 1932)

Pheretima (*Metapheretima*) *elberti* Ude, 1932 : 175.
Metapheretima elberti: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Polypheretima* with paired spermathecal pores about half the body circumference apart in furrows 5/6/7/8/9. Metandric. One pair of presetal genital markings on each of several postclitellar segments.

DESCRIPTION. *External characters.* Length 50–70 mm, diameter 3–4 mm. *C.* 80 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, *c.* 44 on *vii*, *c.* 72 on *xx*, setal ring slightly crowded dorsally on preclitellar segments ($2aa = 2ab = yz = zz$), regular on postclitellar segments ($aa = ab = yz = zz$).

Male pores on short, conical penes within shallow copulatory pouches *c.* 0·35 body circumference apart. Female pore single. Spermathecal pores paired, intersegmental in 5/6/7/8/9, *c.* 0·45 body circumference apart.

Genital markings (Fig. 24d), small, paired, presetal, in line with the spermathecal pores on *vi–ix*, slightly median to the male pores on *xvii*, *xix–xxi*.

Internal characters. Anterior septa posterior to 5/6 present and membranous. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs paired, ventral in *xi*, seminal vesicles large, extending to the dorsal line in *xii*. Pseudoseminal vesicles absent. Copulatory pouches confined to body wall. Spermathecae (Fig. 15i) paired in *vi–ix*.

DISTRIBUTION. Lombok.

REMARKS. The type series could not be located during the preparation of this paper. New material reported here represent the second record for this species.

MATERIAL EXAMINED. *New record.* 2C Lombok; BMNH 1975.7.314.

OTHER RECORDS. Lombok (syntypes of *elberti*).

Polypheretima swelaensis (Ude, 1932)

Pheretima (*Metapheretima*) *swelaensis* Ude, 1932 : 178.
Amynthas swelaensis: Sims & Easton, 1972 : 237.
? *Pheretima* (*Metapheretima*) *badia* (part) Ude, 1932 : 171.

DIAGNOSIS. *Polypheretima* with paired spermathecal pores about one third of the body circumference apart in furrows 5/6/7/8. Metandric. One pair of presetal genital markings on each of several postclitellar segments.

DESCRIPTION. *External characters.* Length *c.* 147 mm, diameter *c.* 5 mm. *c.* 132 segments. Clitellum *xiv–*½*xvi*. First dorsal pore 12/13. Setae, *c.* 80 on *vii*, *c.* 100 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores on squat penes within shallow copulatory pouches *c.* 0·23 body circumference apart. Female pores paired. Spermathecal pores paired, intersegmental in 5/6/7/8, *c.* 0·37 body circumference apart.

Genital markings (Fig. 24c) paired, presetal, slightly median to the spermathecal pores on *vii–ix*; postsetal, median to the spermathecal pores on *vii–viii*; presetal, slightly median to the male pores on *xvii–xx*. Body wall of *xvii–xix* bearing male pores and genital markings elevated to form paired ridges.

Internal characters. Septa 5/6–13/14 present and slightly thickened. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs small, paired ventral in *xi*, seminal vesicles extending to the dorsal line in *xii*. Copulatory pouches shallow, confined to the body wall. Spermathecae (Fig. 15j) paired in *vi–viii*.

DISTRIBUTION. Lombok.

REMARKS. *P. swelaensis* closely resembles *badia* in the form of the male pores and the spermathecae but it may be distinguished by the separation and arrangement of the spermathecal pores and the higher setal numbers of *swelaensis*.

MATERIAL EXAMINED. *New record.* 1C, 1A Lombok; BMNH 1975.7.13–14.

OTHER RECORDS. Lombok (type(s) of *swelaensis*). The two extant members of the type series, Berlin 7215, are here reidentified as *Amynthas* sp. (Both are athecate and precise identification is impractical.) Lombok; (? *badia*: Ude, 1932).

Polypheretima patae species-group

DIAGNOSIS. *Polypheretima* with numerous genital markings arranged in transverse rows. Metandric.

DISTRIBUTION. New Guinea.

SPECIES INCLUDED. *coplandi, huonensis, kershawae, patae.*

REMARKS. The patae species-group contains the metandric *Polypheretima*s from New Guinea. Its members may be recognized by the distributions and separations of the spermathecal pores and, in mature individuals (?), the distribution of genital markings. *P. coplandi*, for example, is known only from four aclitellate specimens which lack genital markings. Marker characters of the species included in the *patae* species-group are given in Table 9. It is noteworthy that in species with less than the full complement of spermathecae, reduction has occurred principally in the posterior thecal segments and not, as is common in other species-groups, in the anterior segments.

The affinities of the *patae* group are with the *badia* species-group which includes the metandric forms from the Lesser Sunda Islands (see numerical studies).

Polypheretima patae sp. nov.

DIAGNOSIS. *Polypheretima* with paired spermathecal pores about half body circumference apart in furrows 4/5/6/7/8/9. Metandric. Genital markings numerous, presetal in transverse rows.

DESCRIPTION. *External characters.* Length *c.* 75 mm, diameter *c.* 3 mm. 86–94 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae 44–48 on *vii*, 46–51 on *xx*, setal ring regular on preclitellar segments ($aa=ab=yz=zz$), with dorsal gaps on postclitellar segments ($aa=ab=yz=\frac{1}{2}zz$).

Male pores on squat penes within copulatory pouches *c.* 0·24 body circumference apart. Female pores paired spermathecal pores paired, intersegmental in 4/5/6/7/8/9, *c.* 0·55 body circumference apart.

Genital markings (Fig. 25a), transverse rows of *c.* 10 small oval papillae, presetal on *ix*, *xvii–xxii*, lateral limits of rows median to the male pores.

Internal characters. Septa 5/6–13/14 membranous. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs paired, extending to the dorsal line in *xi*, seminal vesicles extending to the dorsal line in *xii*. Pseudoseminal vesicles in *xiv*. Copulatory pouches small, only just invading the coelom, penes conical and short. Spermathecae (Fig. 15k) paired in *v–ix*.

DISTRIBUTION. North east New Guinea.

Table 9 Marker characters of the members of the *Polypheretima patae* species-group

Species	Spermathecal furrows	Separation of spermathecal pores	Distribution of genital markings
patae	4/5/6/7/8/9	0·55	presetal only (Fig. 25a)
kershawae	4/5/6/7/8	0·26	pre- and postsetal (Fig. 25b)
coplandi	4/5/6/7	0·42	?
huonensis	5/6/7	0·33	pre- and postsetal (Fig. 25c)

MATERIAL EXAMINED. 1C, 2A In moist soil of dark sandy loam with a high organic matter content and covered with grass and ferns, *c.* 200 m from sea, just north of Bunu village, 50 km north along coast road from Madang, Papua New Guinea, 4° 52′ S, 145° 49′ E, *coll* J W Copland 14 Nov 1971; BMNH 1976.3.186–188 (syntypes of *patae*). 3C, 3A Upper Kaironk valley, Simbai region, Madang district, Papua New Guinea 1900–2100 m, *coll* R N H Bulmer 14 Nov 1973; BMNH 1976.2.22–27.

Polypheretima kershawae sp. nov.

DIAGNOSIS. *Polypheretima* with paired spermathecal pores about one quarter of the body circumference apart in furrows 4/5/6/7/8. Metandric.

Genital markings numerous, pre- and postsetal in transverse rows.

DESCRIPTION. *External characters.* Length 35–45 mm, diameter *c.* 3 mm. *C.* 85 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae *c.* 45 on *vii*, *c.* 41 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores on short conical penes within copulatory pouches *c.* 0·24 body circumference apart. Female pores paired. Spermathecal pores paired, intersegmental in 4/5/6/7/8, 0·26 body circumference apart.

Genital markings (Fig. 25b) small, numerous, arranged in pre- and postsetal rows on *xvii–xx*, lateral limits of rows slightly median to male pores.

Internal characters. Septa 5/6–12/13 slightly thickened. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs paired, large, extending to the dorsal line in *xi*, seminal vesicles in *xii*. Copulatory pouches confined to the body wall. Spermathecae (Fig. 15m) paired in *v–viii*.

DISTRIBUTION. North east New Guinea.

MATERIAL EXAMINED. 4C, 1A Top 15 cm of alluvial clay soil (derived from Gabbro), organic content 15–30% C/N ratio 8 or 9, gentle ridge with mixed montane forest with Podocarpus, Eleocarpacae, Lauacae, Cumoniaceae (dominant), Bismark range, East Highland district, Papua New Guinea, 2500 m, 5° 57′ S, 145° 15′ E, rainfall 900 cm/year, *coll* D R Kershaw 20 Jul 1971; BMNH 1975.5.167–171 (syntypes of *kershawae*). 2C Data as above, *coll* 14 Jul 1971; BMNH 1976.5.172–173. 1C Wau, North east New Guinea, 1200 m, *coll* J Sedlacer 13 Feb 1965; Honolulu.

Polypheretima coplandi sp. nov.

DIAGNOSTIC. *Polypheretima* with paired spermathecal pores about two fifths of the body circumference apart in furrows 4/5/6/7. Metandric.

DESCRIPTION. *External characters.* Length 70–92 mm; the four specimens are aclitellate, mature specimens may be considerably larger. Diameter *c.* 3 mm. *C.* 116 segments. Clitellum not recognizable. Dorsal pores not recognizable anterior to 19/20. Setae 36–38 on *vii*, 28–32 on *xx*, setal ring regular with ventral and dorsal gaps on preclitellar segments ($aa = 1{\cdot}5ab = 1{\cdot}5yz = zz$), dorsal and ventral gaps slightly larger on postclitellar segments ($aa = 2ab = 2yz = zz$).

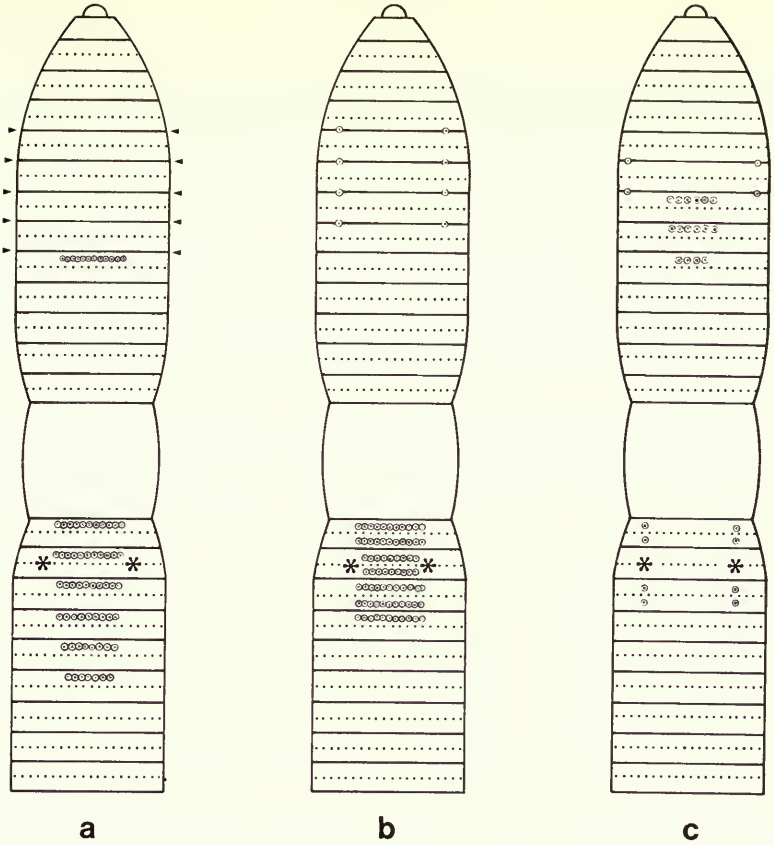

Fig. 25 Anterior ventral surface, diagnostic characters. (For ontogenetic variation of the male pores see Fig. 3.) (a) *Polypheretima patae* sp. nov.; (b) *P. kershawae* sp. nov.; (c) *P. huonensis* sp. nov.

Male pores on squat conical penes within copulatory pouches *c.* 0·19 body circumference apart. Female pores paired. Spermathecal pores paired, intersegmental in 4/5/6/7, *c.* 0·42 body circumference apart.

Genital markings not detected.

Internal characters. Septa 5/6–13/14 membranous. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs paired but linked by a superoesophageal connection, in *xi*, seminal vesicles in *xii*, extending to the dorsal line. Pseudoseminal vesicles in *xiii*. Copulatory pouches confined to the body wall. Spermathecae (Fig. 151) paired in *v–vii*.

DISTRIBUTION. North east New Guinea.

REMARKS. The four specimens on which this species is described lack genital markings. It is probable that mature individuals will possess markings of the type present in other members of the *patae*, species-group.

MATERIAL EXAMINED. 2A Bank of creek, D. A. S. F. Piggery, 3 miles from Goroka township, Eastern Highlands, Papua New Guinea, 6° 02′ S, 145° 22′ E, *coll* J W Copland; BMNH 1976.3.182–183 (syntypes of *coplandi*). 2A Data as above; BMNH 1977.1.213–214.

Polypheretima huonensis sp. nov.

DIAGNOSIS. *Polypheretima* with paired spermathecal pores about one third of the body circumference apart in furrows 5/6/7. Metandric. Genital markings numerous, presetal in transverse rows.

DESCRIPTION. *External characters.* Length *c.* 50 mm, diameter *c.* 3 mm. *C.* 96 segments. Clitellum *xiv–xvi.* First dorsal pore 12/13. Setae, *c.* 39 on *vii* and *xx*, setal ring with dorsal and ventral gaps on preclitellar segments (*aa*=2*ab*=2*yz*=*zz*).

Male pores on squat penes within copulatory pouches *c.* 0·20 body circumference apart. Female pores paired. Spermathecal pores paired, intersegmental in 5/6/7, *c.* 0·33 body circumference apart.

Genital markings (Fig. 25c), transverse rows of *c.* 4 small oval papillae, presetal on *vii–ix*, paired pre- and postsetal papillae on *xvii* and *xix* in line with the male pores.

Internal characters. Septa 5/6–13/14 membranous. Intestine begins in *xv.* Lateral hearts in *x–xii.*

Metandric, testes sacs paired, extending to the dorsal line in *xi*, seminal vesicles extending to the dorsolateral line in *xii.* Pseudoseminal vesicles in *xiv.* Copulatory pouch small, restricted to the body wall, penes conical and short. Spermathecae (Fig. 15n) paired in *vi* and *vii.*

DISTRIBUTION. North east New Guinea.

MATERIAL EXAMINED. 1C Garden soil. Timbe valley, Huon Peninsula, Papua New Guinea, 1500 m, 6° 00′ S, 147° 02′ E, *coll* I L Owen, Aug 1976; BMNH 1977.21.1 (holotype of *huonensis*).

PLANAPHERETIMA Michaelsen, 1934

Megascolex (part): Vaillant, 1889 : 80.
Perichaeta (part): Beddard, 1895 : 388.
Amynthas (part): Beddard, 1900*a* : 612.
Pheretima (part): Michaelsen, 1900 : 234.
Pheretima (*Archipheretima*) (part) Michaelsen, 1928*a* : 7.
Pheretima (*Planapheretima*) Michaelsen, 1934*b* : 15.
Planapheretima: Sims & Easton, 1972 : 209, 233.

TYPE SPECIES. *Pheretima moultoni* Michaelsen, 1913, original designation.

DIAGNOSIS. Megascolecidae with an oesophageal gizzard in *viii.* Intestinal caeca sometimes present, intestinal walls often with glandular areas, intestinal gizzards absent. Body mainly flattened dorsoventrally, setae usually crowded ventrally, creeping sole often present. Male pores simple, never within copulatory pouches. Spermathecal diverticular simple, usually ectal in origin.

DESCRIPTION. Body cylindrical or flattened dorsoventrally, often with a glandular ventral surface (creeping sole) on the anterior region of the body. Clitellum annular, extending over three or more segments (*xiii, xiv–xvi, xvii*). First dorsal pore between 6/7 and 12/13. Setae perichaetine, evenly distributed round each segment or crowded, often densely, on the ventral surface. Lateral hearts in *x–xii* and sometimes *xiii.*

Oesophagus with a well-developed gizzard in *viii*; calciferous glands and dorsal pouches absent. Intestine begins in *xiv, xv* or *xvi*, often modified by the development of glandular walls or a pair of lateral caeca, intestinal gizzards absent. In the absence of externally recognizable adaptations to arboreal life, the presence of glandular intestinal walls may be used to recognize Chinese members of this genus.

Holandric. The testes of each segment are enclosed in single or paired stout sacs which usually occupy most of the coelom and often enclose the anterior seminal vesicles and the lateral hearts of *x* and *xi.* Seminal vesicles paired in *xi* and *xii.* Prostates racemose. Paired combined male and prostatic pores on the ventral surface of *xviii* in the setal ring. Male pores usually simple or on circular porophores, rarely on slim superficial penes (Fig. 29a), on penes carried on circular porophores (Fig. 3g) or on a raised area (Fig. 29b). Copulatory pouches absent. Ovaries free in *xiii.* Oviducts lead to single or closely paired, midventral, equatorial pore(s) on *xiv.* Spermathecae each differentiated into duct and ampulla; diverticula simple, usually ectal in origin and usually as long as or longer than the main duct and ampulla. Spermathecae arranged in pairs in one to five adjacent segments between *v* and *ix.* Spermathecal pores small or small slitlike openings, always intersegmental.

Genital markings of the discrete type or annular ridges; diffuse markings absent. Discrete genital markings may be single or paired, segmental or intersegmental, they are never random or numerous (cf. *Polypheretima bifaria* and *patae* species-group). The glandular tissue associated with the genital markings is usually restricted to the body wall and only rarely invades the coelom in the form of a stalked gland. The area around the male pores may be infrequently elevated above the body surface.

DISTRIBUTION. (Fig. 7.) In areas of high humidity in China, Burma, Sumatra, Borneo, Celebes and New Guinea.

NUMERICAL STUDIES. The taxa of the genus *Planapheretima* listed in Table 1 (72–85) were subjected to a numerical analysis utilizing the characters listed in Table 2. The configuration of taxa with the first and third vectors of the principle co-ordinate analysis employed as axes produced the greatest degree of clustering. The use of the first and second vectors produced similar but more diffuse clusters. Recognition of the clusters is considerably enhanced by the addition of the MST with graded linkages (Fig. 26).

Two divisions, indicated by circular and square symbols, may be recognized. The taxa of Division I from the Indo-Australasian archipelago (indicated by circular symbols) all have simple intestines while those of Division II from Asia (square symbols) have intestines modified by the development of glandular walls and/or intestinal caeca.

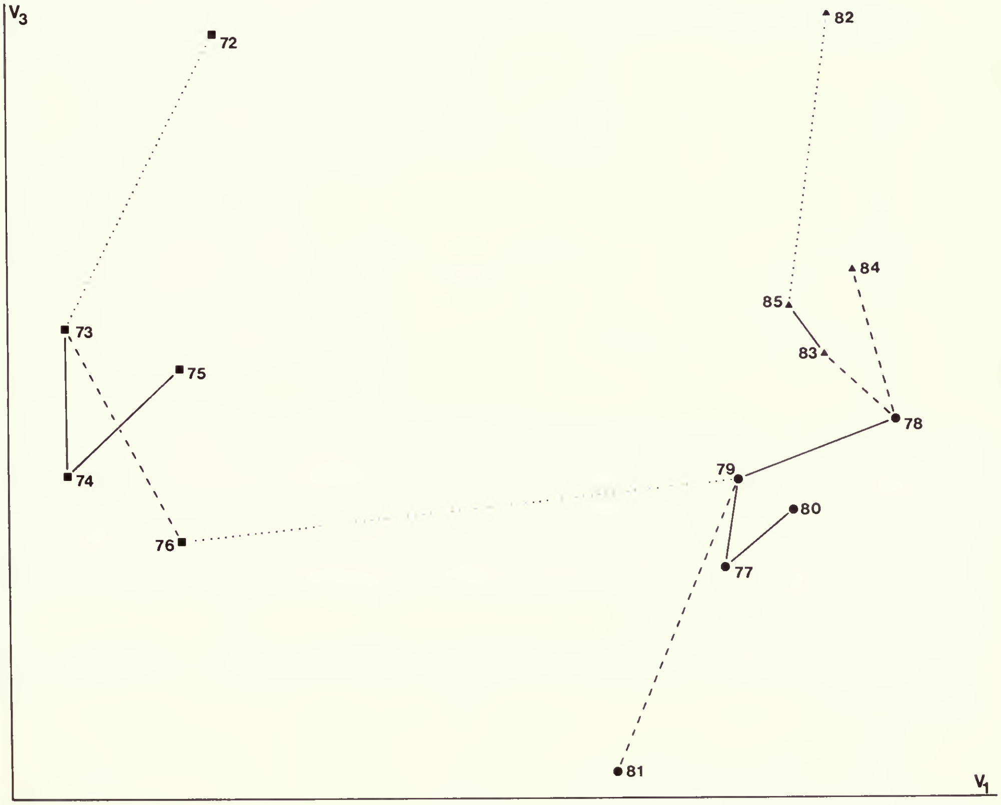

Fig. 26 Principal co-ordinates analysis of 14 species here assigned to *Planapheretima* (72–85 of Table 1): the configuration of species with the vectors corresponding to the first and third latent roots. The linkages of the added MST are graded to indicate percentage similarities; ——, +90%; - - - - -, 85–90%, · · · · ·, −85%. Two major assemblages are recognized:
Division I – circular and triangular symbols (circles – *subulata* species-group, triangles – species allied to the *subulata* species- group).
Division II – square symbols (*bambophila* species-group).

Division I contains five taxa (indicated by solid circular symbols), they are situated close together on the first and third vectors and possess relatively high mutual MST linkages. Morphologically these taxa are similar in having simple male pores on circular porophores and (when present) paired genital markings; all are assigned to the *subulata* species-group. The other four taxa of Division I (indicated by open circular symbols) have, with the exception of 83 and 85, lower MST linkages. Unlike the taxa of the *subulata* species-group, they exhibit considerable diversity in the form of the male pores and the genital markings. It is proposed to consider each as a separate species.

It has not been possible to examine any representatives of the taxa of Division II before the numerical studies were undertaken so assessments were derived from the original descriptions (Gates, 1972 : 169 in the case of *arboricola*). All are now assigned to the *continens* species-group.

A summary of the phenetic classification based on this numerical investigation is given in Table 10.

Table 10 Phenetic classification and checklist of the genus *Planapheretima*

DIVISION I	*subulata* species-group	*celebensis* (77)
		moultoni (78)
		pallenscens (79)
		rufomaculata (80)
		subulata (81)
		ambulatrix (82)
		hasselti (83)
		maculata (84)
		nieuwenhuisi (85)
		sera
DIVISION II	*bambophila* species-group	*arboricola* (76)
		bambophila (75)
		continens (72)
		lacertina (73)
		tenebrica (74)

Numbers in parentheses indicate taxa assessed in numerical studies (see Figs 6 and 26).

REMARKS. It is clear from the general numerical study (see above) that the acaecate and caecate species included in this genus form a single phenetic group, distinct from all of the other acaecate species assessed. However, in the absence of representatives of the caecate genera from these computations, no information is available about the affinities of the caecate members of *Planapheretima* with the caecate genera of the *Pheretima* group. Unfortunately the two representatives of *Planapheretima* which were included in the general appraisal of the *Pheretima* group by Sims & Easton (1972) were both acaecate.

In *P. moultoni* and *celebensis*, paired, intersegmental markings are closely associated with the male pores and superficially resemble the crescentic markings found in *Metapheretima* and *Pleionogaster*.

Key to the species of the genus *Planapheretima*

1	First spermathecal pores in furrow 4/5	2
	First spermathecal pores in furrow 5/6	5
	First spermathecal pores in furrow 6/7	8
	First spermathecal pores in furrow 7/8	10
2	Three thecal segments	3
	Five thecal segments	***subulata*** (p. 69)
3	Intestinal caeca absent (Borneo)	4
	Intestinal caeca present (rudimentary) (China)	***continens*** (part) (p. 75)

4	Spermathecae as Fig. 27a	***moultoni*** (p. 68)
	Spermathecae as Fig. 27b	***pallescens*** (p. 68)
5(1)	One thecal segment	***rufomaculata*** (p. 71)
	Two thecal segments	***hasselti*** (p. 71)
	Three thecal segments	***continens*** (part) (p. 75)
	Four thecal segments	6
6	Intestinal caeca absent	7
	Intestinal caeca simple, rudimentary	***lacertina*** (p. 77)
	Intestinal caeca multiple	***arboricola*** (p. 76)
7	Spermathecal pores lateral; intestinal wall simple (Celebes)	***celebensis*** (p. 70)
	Spermathecal pores ventrolateral; intestinal wall glandular in segments *xx–xc* (China)	***tenibrica*** (p. 78)
8(1)	One thecal segment	9
	Two thecal segments	***ambulatrix*** (p. 71)
9	Postclitellar genital field as Fig. 29c	***maculata*** (p. 73)
	Postclitellar genital field as Fig. 30c	***sera*** (p. 73)
10(1)	Males pores *c.* 0·15 body circumference apart; postclitellar genital markings (Fig. 29d) single, median presetal (Borneo)	***nieuwenhuisi*** (p. 74)
	Male pores *c.* 0·25 body circumference apart; postclitellar genital markings not of this form or absent (China)	***bambophila*** (p. 78)

Planapheretima subulata species-group

DIAGNOSIS. *Planapheretima* with simple intestines lacking glandular walls and caeca. Male pores on simple porophores, genital markings paired.

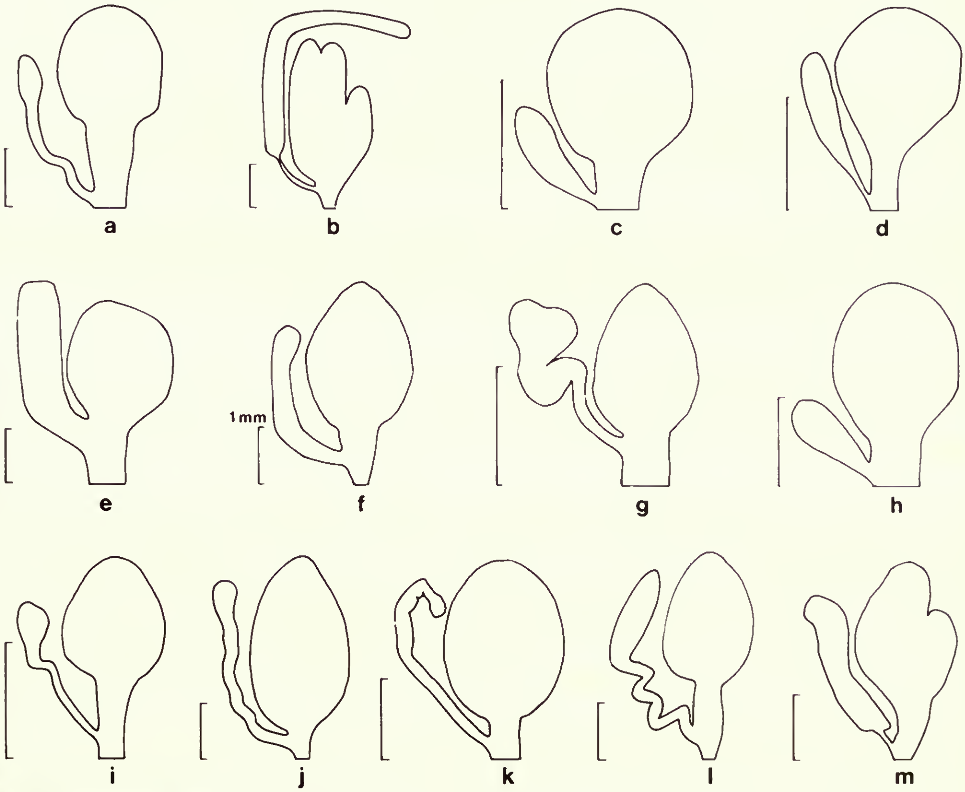

Fig. 27 Spermathecae. (a) *Planapheretima moultoni*; (b) *P. pallescens*; (c) *P. subulata*; (d) *P. celebensis*; (e) *P. ambulatrix*; (f) *P. hasselti*; (g) *P. maculata*; (h) *P. nieuwenhuisi*; (i) *P. continens*; (j) *P. arboricola*; (k) *P. lacertina*; (l) *P. tenebrica*; (m) *P. bamophilia*. All scales 0·5 mm unless otherwise indicated. (See also Fig. 30f.)

DISTRIBUTION. Borneo, Celebes, New Guinea.

SPECIES INCLUDED. *celebensis, moultoni, pallescens, rufomaculata, subulata.*

REMARKS. Most of the species included within the *subulata* species-group are readily distinguishable on the distribution of their spermathecal pores; *subulata* 5 pairs 4/5/6/7/8/9, *celebensis* 4 pairs 5/6/7/8/9, *moultoni* and *pallescens* 3 pairs 4/5/6/7 and *rufomaculata* 1 pair 5/6. The affinities of *moultoni* and *pallescens* are discussed below (see remarks of *moultoni*).

Planapheretima moultoni (Michaelsen, 1913)

Pheretima moultoni Michaelsen, 1913*b* : 90; Michaelsen, 1914 : 59.
Pheretina (*Archipheretima*) *moultoni*: Michaelsen, 1928*a* : 14.
Pheretima (*Planapheretima*) *moultoni*: Michaelsen, 1934*b* : 15.
Planapheretima moultoni: Sims & Easton, 1972 : 209, 233.

DIAGNOSIS. *Planapheretima* with a simple intestine; spermathecal pores in furrows 4/5/6/7. Spermathecae as Fig. 27a.

DESCRIPTION. *External characters.* Length 45–55 mm, diameter 2–2·5 mm 93–100 segments. Body depressed, concave ventrally, with creeping sole. Colouration; light yellowish grey with up to 20 small dark violet-brown or nearly black spots around each dorsal pore, the spots fusing to form a ring with the pore marked by a white spot, the rings fuse to form a median line which becomes larger posteriorly, the number of irregular spots diminish posteriorly as well. Clitellum ½*xiii–xvi*. First dorsal pore 9/10. Setae *c.* 100 on each segment, setal ring crowded ventrally without dorsal or ventral gaps (*5aa*=*5ab*=*yz*=*zz*).

Male pores on slightly raised conical porophores *c.* 0·30 body cirumference apart. Female pore single. Spermathecal pores small in 4/5/6/7, *c.* 0·33 body circumference apart.

Genital markings (Fig. 28a) paired, pre- and postsetal, slightly median to the male pores on *xviii.*

Internal characters. Anterior septa delicate, some in the region of the gizzard possibly absent. Intestine simple, begins in *xv*. Lateral hearts in *x–xiii.*

Holandric, testes sacs paired, large in *x* and *xi*, seminal vesicles small, extending to the lateral line in *xi* and *xii*. Spermathecae (Fig. 27*a*) paired in *v–vii.*

DISTRIBUTION. Borneo.

REMARKS. *P. moultoni* and *pallescens* may be distinguished only by the form of the spermathecae and the absence of genital markings in *pallescens.* Since the holotype of *pallescens* has been dissected nearly to destruction, it is difficult to assess the validity of these distinctions and possibly when more material becomes available for study, *pallescens* may prove to be a junior synonym of *moultoni.*

MATERIAL EXAMINED. 2C Mt Poi, Sarawak; Hamburg v8090 (syntypes of *moultoni*). 3C, 2A Mt Poi, Sarawak; Hamburg v10510 (*moultoni*: Michaelsen, 1928).

Planapheretima pallescens (Michaelsen, 1928)

Pheretima (*Archipheretima*) *pallescens* Michaelsen, 1928*a* : 15.
Pheretima (*Planapheretima*) *pallescens*: Michaelsen, 1934*b* : 15.
Planapheretima pallescens: Sims & Easton, 1972 : 231.

DIAGNOSIS. *Planapheretima* with a simple intestine; spermathecal pores in furrows 4/5/6/7. Spermathecae as Fig. 27b.

DESCRIPTION. *External characters.* Length *c.* 60 mm (aclitellate), diameter *c.* 2·2 mm. *C.* 96 segments. Body depressed ventrally, creeping sole on *xvi–xx*. Colouration; bright yellow with a reddish, mother of pearl lustre and a sparsely developed brown, irregularly defined line on the anterior segments of the body. Clitellum not developed. First dorsal pore at either 10/11 or 11/12. Setae, *c.* 122 on *v*, *c.* 141 on *ix*, *c.* 134 on *xvii.*

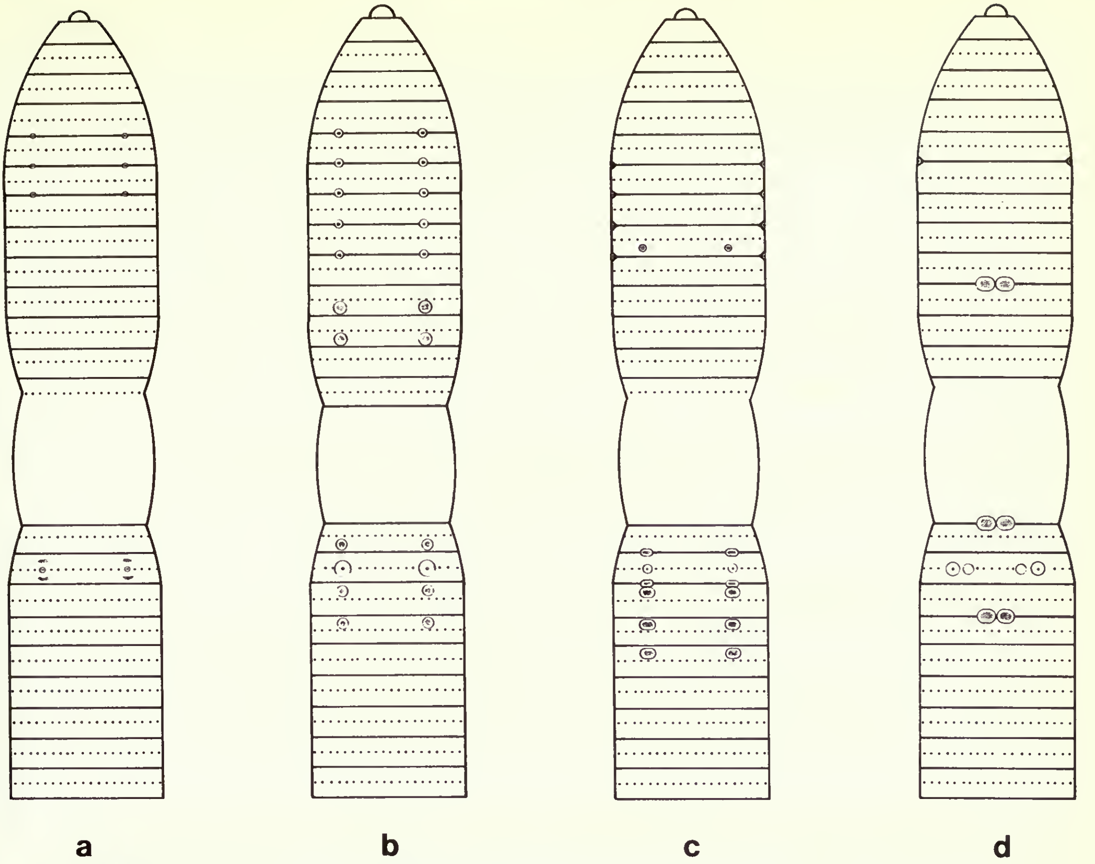

Fig. 28 Anterior ventral surface, diagnostic characters. (a) *Planapheretima moultoni*; (b) *P. subulata*; (c) *P. celebensis*; (d) *P. rufomaculata.*

Male pores on small porophores outside the region of the creeping sole, *c.* 0·33 body circumference apart. Female pore(s) not recorded. Spermathecal pores in 4/5/6/7, *c.* 0·33 body circumference apart.

Genital markings not detectable.

Internal characters. Anterior septa delicate, 8/9/10 not detected and probably absent. Beginning of intestine not recorded. Intestine simple. Disposition of lateral hearts not recorded.

Holandric, testes sacs large, paired in *x* and *xi*, seminal vesicles small in *xi* and *xii*. Spermathecae (Fig. 27b), paired in *v–vii*.

Description after Michaelsen (1928); and the author after examination of the remains of the holotype.

DISTRIBUTION. Borneo.

REMARKS. This species is similar to *moultoni* with which it may be conspecific (see above).

MATERIAL EXAMINED. 4 spermathecae, gizzard, oesophagus, part of anterior intestine and anterior male reproductive system, Mt Penrissen, Sarawak; Hamburg v10522 (remains of holotype of *pallescens*).

Planapheretima subulata (Michaelsen, 1899)

Amynthas subulatus Michaelsen, 1899 : 29; Beddard, 1900*a* : 641.
Pheretima subulata: Michaelsen, 1900 : 307.
Metapheretima subulata: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Planapheretima* with a simple intestine; spermathecal pores in furrows 4/5/6/7/8/9.

DESCRIPTION. *External characters.* Length 60–70 mm, diameter *c.* 3 mm. 105–106 segments. Body flattened, concave ventrally, creeping sole poorly developed. Colouration; (preserved specimen), brownish dorsally, light yellowish white ventrally, clitellum yellowish grey. Clitellum *xiv–xvi*. First dorsal pore 6/7. Setae, *c.* 80 on *vii*, *c.* 60 on *xx*, setal ring crowded ventrally with dorsal gaps on preclitellar segments ($4aa=4ab=yz=0{\cdot}5zz$), without dorsal or ventral gaps on postclitellar segments ($4aa=4ab=yz=zz$).

Male pores at the centre of large circular porophores *c.* 0·30 body circumference apart. Female pores paired. Spermathecal pores large in furrows 4/5/6/7/8/9, *c.* 0·30 body circumference apart.

Genital markings (Fig. 28b) paired, in line with the male pores, presetal on *xix* and *xx*, postsetal on *x*, *xi* and *xvii*.

Internal characters. Anterior septa present and delicate. Intestine simple, begins in *xvi*. Lateral hearts in *x–xii*.

Holandric, testes sacs large, paired, extending to the dorsal line, in *x* and *xi*, seminal vesicles large, extending to the dorsal line in *xi* and *xii*. Spermathecae (Fig. 27c), paired in *v–ix*.

DISTRIBUTION. Celebes.

REMARKS. Sims & Easton (1972) placed this species in *Metapheretima* on the basis of its original description but the subsequent examination of the type series revealed the depressed body, crowded ventral setae and creeping sole which characterize the genus *Planapheretima*.

MATERIAL EXAMINED. 1C Central Celebes; Hamburg v5192 (syntypes of *subulata*). 2C 1A Central Celebes; Hamburg v5193 (syntypes of *subulata*).

The original description of this species was based on two series of specimens, both collected by P. & U. Sarasin in February 1895 from central Celebes. The localities were: Hill country in the region of the Kalaena river, *c.* 400 m, 5 Feb 1895 and southern foothills of Takalekadjo, *c.* 1000 m, 7 Feb 1895. Although the labels clearly indicate that these specimens were collected in central Celebes by P. and M. Sarasin, they do not indicate from which locality each series originated.

Planapheretima celebensis (Michaelsen, 1899)

Amynthas celebensis Michaelsen, 1899 : 32; Beddard, 1900*a* : 642.
Pheretima celebensis : Michaelsen, 1900 : 261.
Planapheretima celebensis: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Planapheretima* with simple intestine; spermathecal pores in furrows 5/6/7/8/9.

DESCRIPTION. *External characters.* Length *c.* 60 mm, diameter *c.* 2 mm, *C.* 90 segments. Shape of body and form of ventral surface not recorded. Colouration; (preserved specimen) bright brownish yellow dorsally, grey ventrally, clitellum dark violet grey. Clitellum $\frac{2}{3}$*xiii–xvi*. First dorsal pore 6/7. Setae, *c.* 49 on *vi*, *c.* 48 on *x*, *c.* 40 on *xvii*, *c.* 44 on *xxvi*, setal ring crowded ventrally ($3ab=yz$).

Male pores on oval porophores *c.* 0·29 body circumference apart. Female pore(s) not recorded. Spermathecal pores in furrows 5/6/7/8/9, *c.* 0·50 body circumference apart.

Genital markings (Fig. 28c) paired, in line with the male pores, presetal on *xix–xxi*, postsetal on *viii*, intersegmental at 17/18, 18/19.

Internal characters. Anterior septa present and delicate. Beginning of intestine not recorded. Intestine simple. Lateral hearts in *x–xiii*.

Holandric, testes sacs paired, large in *x* and *xi*, seminal vesicles in *xi* and *xii*. Spermathecae (Fig. 27d) paired in *vi–ix*.

Description based on Michaelsen, 1899, 1900; Fig. 28c is an interpretation of the genital field based on the written description.

DISTRIBUTION. Celebes.

RECORDS. 1C Takalekadjo range, central Celebes; Hamburg v5188 (holotype of *celebensis*). Although this specimen is listed in the catalogue of the Hamburg Museum it could not be located during the preparation of this paper: Dr M. Dzwillo, personal communication.

Planapheretima rufomaculata (Gates, 1948)

Planapheretima rufomaculata Gates, 1948 : 162.
Planapheretima rufomaculata: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Planapheretima* with a simple intestine; spermathecal pores in furrow 5/6 only.

DESCRIPTION. *External characters.* Length 43–45 mm, diameter *c.* 4 mm. Segment number not recorded. Body depressed, creeping sole not recognized. Colouration; pigmentation restricted to three longitudinal, irregular stripes, a median dorsal dark red stripe and two lateral light red stripes. Clitellum ⅓*xiii–xvi.* First dorsal pore 11/12. Setal numbers not recorded, setal ring crowded ventrally.

Male pores on circular, widely spaced, porophores separated by 25–26 setae. Female pore single. Spermathecal pores in 5/6, *c.* 0·50 body circumference apart.

Genital markings (Fig. 28d) closely paired, intersegmental at 9/10, 16/17 and 19/20, segmental, slightly median to male pores on *xviii.*

Internal characters. Anterior septa present and delicate. Intestine simple, begins in *xv.* Lateral hearts in *ix–xiii.*

Holandric, testes sacs single, U-shaped, extending to the dorsal line in *x*, those of *xi* not seen but assumed to be similar, seminal vesicles in *xi* and *xii*, details not recorded. Spermathecae, paired in *vi*, duct as long as main ampulla, diverticulum ental, tubular, nearly as long as main axis.

Stalked glands associated with the genital markings.

Description after Gates, 1948; Fig. 28d is an interpretation of the genital field based on the written description.

DISTRIBUTION. New Guinea.

RECORDS. 2C Near Idenburg river, West Irian (holotype and paratype of *rufomaculata*). The type series of this species is absent from the collections of the Museum Zoologicum Bogoriense where Reynolds & Cook (1976) stated it had been deposited: Dr S. Kadarsan, personal communication.

Planapheretima ambulatrix (Michaelsen, 1934)

Pheretima (*Planapheretima*) *ambulatrix* Michaelsen, 1934*b* : 22.
Planapheretima ambulatrix: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Planapheretima* with a simple intestine; spermathecal pores in furrows 6/7/8.

DESCRIPTION. *External characters.* Length *c.* 55 mm, diameter *c.* 2·5 mm. *C.* 100 segments. Body depressed with a creeping sole occupying the whole ventral surface. Colouration; (preserved specimen) yellowish to yellowish grey without pigmentation. Clitellum ½*xiii–xvii.* First dorsal pore not recognized. Setae, *c.* 120 on *vii*, *c.* 130 on *xx*, setal ring crowded ventrally without dorsal or ventral gaps (5*aa*=5*ab*=*yz*=*zz*).

Male pores on minute elongate penes *c.* 0·25 body circumference apart (Fig. 29a). Female pore(s) not recognized. Spermathecal pores small in 6/7/8, *c.* 0·25 body circumference apart.

Genital markings not recognized.

Internal characters. Anterior septa present and delicate. Intestine simple, begins in *xvi.* Lateral hearts in *x–xii.*

Holandric, testes sacs simple, U-shaped and large in *x* and *xi*, seminal vesicles extending to the dorsal line in *xi* and *xii.* Spermathecae (Fig. 27e) paired in *vii* and *viii.*

DISTRIBUTION. Borneo.

MATERIAL EXAMINED. 1C 5A Mt Dulit, Sarawak; BMNH 1933.10.6.6 (holotype and paratypes of *ambulatrix*). 2A Data as above; Hamburg v11955 (paratypes of *ambulatrix*).

Planapheretima hasselti (Horst, 1883)

Megascolex hasselti Horst, 1883 : 190; Vaillant, 1889 : 80.
Perichaeta hasselti: Horst, 1885 : 5; Beddard, 1895 : 426.

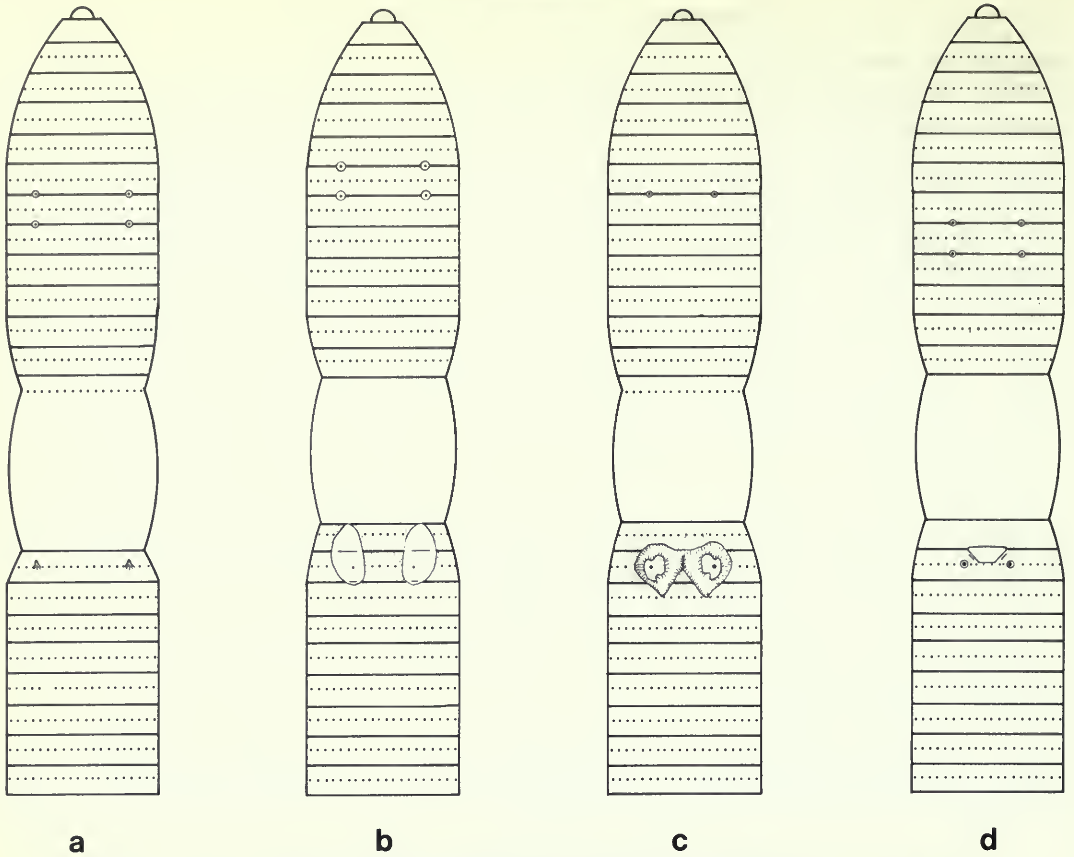

Fig. 29 Anterior ventral surface, diagnostic characters. (a) *Planapheretima ambulatrix*; (b) *P. hasselti*; (c) *P. maculata*; (d) *P. nieuwenhuisi*.

Amynthas hasselti: Beddard, 1900*a* : 638.
Pheretima hasselti: Michaelsen, 1900 : 271 [non Michaelsen, 1922 : 30 (=*Amynthas morrisi* species-group)].
Planapheretima hasselti: Sims & Easton, 1972 : 180, 233.
Pheretima (*Planapheretima*) *frondicola* Michaelsen, 1934*b* : 17.
Planapheretima frondicola: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Planapheretima* with a simple intestine; spermathecal pores in furrows 5/6/7.

DESCRIPTION. *External characters.* Length 50–54 mm, diameter 2–3 mm. 90–95 segments. Body depressed with a creeping sole occupying the ventral surface. Colouration; (preserved specimen), pale yellowish grey or grey with lighter intersegmental furrows. Clitellum *xiii–xvi*. First dorsal pore 12/13. Setae, *c.* 110 on *vii*, *c.* 70 on *xx*, setal ring crowded ventrally without dorsal or ventral gaps (*6aa*=*6ab*=*yz*=*zz*).

Male pores simple, *c.* 0·13 body circumference apart on large, oval porophores extending onto *xvii* and *xix* (Fig. 29b). Female pore single. Spermathecal pores large in 5/6/7, *c.* 0·22 body circumference apart.

Genital markings absent.

Internal characters. Anterior septa present and delicate. Intestine simple, begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs paired, large, extending to the dorsal line in *x* and *xi*, seminal vesicles of *xi* small, extending to the lateral line, those of *xii* larger, extending to the dorsal line. Spermathecae (Fig. 27f) paired in *vi* and *vii*, Distribution. Sumatra and Borneo.

Remarks. The material identified as *hasselti* by Michaelsen (1922) is here assigned to the *Amynthas morrisi* species-group since it lacks a depressed body, has crowded ventral setae and paired intestinal caeca—confirmed by examination of Michaelsen's material: Leiden, 1854.

The species *frondicola* has been included within the synonymy of *hasselti* since the two type series differ from each other only in that the clitellum is longer and the raised areas bearing the male pores are more fully developed in *frondicola.*

This is the only representative of *Planapheretima* recorded from Sumatra.

Material examined. 2C Lebang, Sumatra; Leiden 1853 (holotype of *hasselti*). 1C, 1A Mt Dulit, Sarawak; BMNH 1933.10.6.9 (syntypes of *frondicola*). 2A Locality as above; Hamburg v11957 (syntypes of *frondicola*).

Planapheretima sera sp. nov.

Diagnosis. *Planapheretima* with a simple intestine; spermathecal pores in furrow 6/7 only. Male pores on elongate porophores (Fig. 30c).

Description. *External characters*. Length *c.* 78 mm, diameter *c.* 3 mm. *C.* 115 segments. Body depressed, creeping sole present on postclitellar segments. Colouration; yellowish brown with dark brown or red spots on dorsal and lateral surfaces, clitellum purple. Clitellum $\frac{3}{4}$*xiii–xvi.* First dorsal pore 8/9 or 9/10. Setae *c.* 70 on *vii* and *xx*, setal ring crowded ventrally without dorsal or ventral gaps ($5aa=5ab=yz=zz$).

Male pores postsetal on large oval posteriorly directed porophores which occupy the whole length of the segment, *c.* 0·20 body circumference apart. Female pore(s) not seen. Spermathecal pores small in 6/7, *c.* 0·40 body circumference apart.

Genital markings (Fig. 30c) paired, presetal, in line with the male pores on *xix* and *xx*.

Internal characters. Anterior septa present and delicate. Intestine simple, begins in *xv*. Lateral hearts in *x–xiii.*

Holandric, testes sacs single, U-shaped, extending to the dorsolateral line in *x* and *xi*, seminal vesicles in *xi* and *xii*, those of *xi* enclosed in the testes sacs. Spermathecae (Fig. 30f) paired in *vii*, diverticulum very long, convoluted.

Distribution. Borneo.

Material examined. 1C On ivy-like leaf of 20 m tall shrub, near old campsite, Royal Geographical Society camp 4, ridge top forest, Gunong Mulu, Sarawak, altitude 1970 m, 4° 02′N, 114° 54′ E, *coll* J Dring 2030 hrs, 22 Aug 1977; BMNH 1977.21.2 (holotype of *sera*). 1C On leaf of herb, 1 m up bank of dried up temporary stream, Royal Geographical Society camp 3, Gunong Mulu, Sarawak, altitude 1450 m, *coll* J Dring 2100 hrs, 9 Sep 1977; BMNH 1977.212 (paratype of *sera*).

Planapheretima maculata (Ude, 1925)

Pheretima maculata Ude, 1925 : 104.
Pheretima (*Archipheretima*) *maculata*: Michaelsen, 1928*a* : 18; Ude, 1932 : 120.
Pheretima (*Planapheretima*) *maculata*: Michaelsen, 1934*b* : 15.
Planapheretima maculata: Sims & Easton, 1972 : 233.
Pheretima (*Archipheretima*) *scandens* Michaelsen, 1928*a* : 18.
Pheretima (*Planapheretima*) *scandens*: Michaelsen, 1934*b* : 15.
Planaphertima scandens: Sims & Easton, 1972 : 233.

Diagnosis. *Planapheretima* with a simple intestine; spermathecal pores in furrow 6/7 only. Male pores surrounded by annular ridges (Fig. 29c).

Description. *External characters*. Length 30–40 mm, diameter 2–3 mm. 50–77 segments. Body depressed with creeping sole on the ventral surface. Colouration; whole body highly iridescent, yellowish brown with, on the dorsal surface, irregularly arranged rust-red or dark brown spots which form a ring-shaped pattern around each dorsal pore, clitellum violet brown. Clitellum $\frac{1}{3}$ *xiii–xvi*. First dorsal pore 9/10 or 10/11. Setae, 40–59 on *vii* and *xx*, setal ring crowded ventrally without dorsal or ventral gaps (5*aa*=5*ab*=*yz*=*zz*).

Male pores simple, *c.* 0·33 body circumference apart. Female pore single. Spermathecal pores small in 6/7, *c.* 0·33 body circumference apart.

Genital markings (Fig. 29c) in the form of a ridge surrounding each male pore.

Internal characters. Anterior septa delicate, 8/9 absent. Intestine simple, begins in *xv*. Lateral hearts in *xi–xiii* and possibly *x*.

Holandric, testes sacs paired, large in *x* and *xi*; seminal vesicles in *xi* and *xii*, those of *xi* enclosed in the testes sacs of that segment. Spermathecae (Fig. 27g) paired in *vii*.

DISTRIBUTION. Borneo.

REMARKS. The type series of *scandens* differs from the original description of *maculata* in the form of the spermathecal diverticulum, this difference is considered insufficient to justify the separation of two forms.

MATERIAL EXAMINED. 1C Mt Penrissen, Sarawak; Hamburg v10515 (holotype of *scandens*).

OTHER RECORDS. Mt Murud, Brunei; (type(s) of *maculata*).

Planapheretima nieuwenhuisi (Michaelsen, 1922)

Pheretima nieuwenhuisi Michaelsen, 1922 : 47.
Pheretima (*Archipheretima*) *nieuwenhuisi*: Michaelsen, 1928*a* : 22.
Pheretima (*Planapheretima*) *nieuwenhuisi*: Michaelsen, 1934*b* : 15.
Planapheretima nieuwenhuisi: Sims & Easton, 1972 : 181, 233.

DIAGNOSIS. *Planapheretima* with a simple intestine; spermathecal pores in furrows 7/8/9.

DESCRIPTION. *External characters.* Length *c.* 44 mm, diameter *c.* 2 mm. *C.* 92 segments. Body depressed with a distinct creeping sole. Colouration; body an intense chestnut brown or maroon becoming more greyish at the anterior and posterior ends, clitellum a bright bluish slate-grey. Clitellum *xiii–xvi*. First dorsal pore 9/10. Setae, *c.* 75 on *vii* and *xx*. Setal ring crowded ventrally without dorsal or ventral gaps (5*aa*=5*ab*=*yz*=*zz*).

Male pores simple, *c.* 0·15 body circumference apart. Female pore single. Spermathecal pores small in 7/8/9, *c.* 0·20 body circumference apart.

Genital markings (Fig. 29d) single, median, intersegmental at 17/18.

Internal characters. Anterior septa present and delicate. Intestine simple, begins in *xiv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs paired, extending to the dorsal line in *x* and *xi*, seminal vesicles of *xi* small, enclosed in the testes sacs of that segment, those of *xii* larger, extending to the dorsal line. Spermathecae (Fig. 27h) paired in *viii* and *ix*.

DISTRIBUTION. Borneo.

MATERIAL EXAMINED. 1C (lacking most of the internal anterior anatomy and parts of the body wall), Mt Damoes, 'Borneo' (? Kalimanton); Leiden 1811 (part of holotype of *nieuwenhuisi*). Gizzard, oesophagus, anterior portion of intestine, anterior male reproductive system and two fragments of body wall, data as above; Hamburg v9306 (part of holotype of *nieuwenhuisi*).

Planapheretima bambophila species-group

DIAGNOSIS. *Planapheretima* with an intestine modified in the anterior region by the presence of caeca or glandular walls or both.

DISTRIBUTION. Burma, China.

SPECIES INCLUDED. *arboricola*, *bambophila*, *continens*, *lacertina*, *tenebrica*.

REMARKS. The members of this species-group have caeca and/or glandular areas on the walls of the intestine; all occur on the mainland of Asia. In contrast, species outside of this species-group

(*P. subulata* species-group and its allies) have unmodified intestines and occur in the Indo-Australasian Archipelago.

As discussed above (see numerical studies) the five species comprising this species-group appear to be closely related although there are both caecate and acaecate forms from edaphic and arboricolous habitats. Despite the five species having apparently only convergent features in common with the other members of the genus, the generic diagnosis of *Planapheretima* has been widened to accommodate them, since I do not propose to elevate the group to generic status on current evidence. More morphological information is required while the genus *Amynthas*, with which this group seemingly has affinities, needs to be thoroughly revised.

In addition to the species included in the *bambophila* species-group, two others, *acidophila* and *jaoi*, have been recorded from arboricolous habitats in Szechwan. As neither is adapted morphologically to an arboreal mode of life nor is either apparently related to any of the species of the *bambophila* species-group, it is proposed that they should remain in *Amynthas* where they were placed by Sims & Easton (1972).

Knowledge of the Chinese members of the *bambophila* species-group derives from the original descriptions of the species (Chen, 1946). Several discrepancies in the separation of the male and spermathecal pores exist in these accounts so caution needs to be taken when identifying species of this group.

Marker characters of the species assigned to the *bambophila* species-group are given in Table 11.

Table 11 Marker characters of the members of the *Planapheretime bambophila* species-group

Species	Spermathecal furrows	Intestinal caeca	Distribution
continens	4/5/6/7 or 5/6/7/8	rudimentary	Szechwan
lacertina	5/6/7/8/9	rudimentary	Szechwan
arboricola	5/6/7/8/9	multiple	Burma
tenebrica	5/6/7/8/9	absent	Szechwan
bambophila	7/8/9	absent	Szechwan

Planapheretima continens (Chen, 1946)

Pheretima continens Chen, 1946 : 95.
Amynthas continens: Sims & Easton, 1972 : 235.

DIAGNOSIS. *Planapheretima* with rudimentary intestinal caeca; spermathecal pores in furrows 4/5/6/7 or 5/6/7/8.

DESCRIPTION. *External characters.* Length 33–38 mm, diameter *c.* 2 mm. 94–102 segments. Body cylindrical, creeping sole absent. Colouration; grey on dorsal surface, pale ventrally, clitellum light chocolate red. Clitellum $\frac{1}{2}$*xiii–xvii*. First dorsal pore 11/12. Setae, 30–40 on *iii*, 54–58 on *vii*, 52–55 on *xxv*, setal ring slightly crowded ventrally with slight dorsal and ventral gaps ($aa = 1{\cdot}2ab = 1{\cdot}5yz = zz$).

Male pores on small penes which arise from circular porophores *c.* 0·33 body circumference apart. Female pore(s) not recorded. Spermathecal pores small in 5/6/7/8 or occasionally 4/5/6/7, *c.* 0·40 body circumference apart.

Genital markings (Fig. 30*b*) paired, presetal on *ix* slightly median to the line of the spermathecal pores.

Internal characters. Septa 5/6–7/8 thickened, 8/9/10 absent, 10/11 membranous, 11/12–14/15 thickened. Intestine begins in *xvi* with paired rudimentary caeca about one segment long (origin not recorded) and with glandular walls posterioriad to the caeca. Disposition of lateral hearts not recorded.

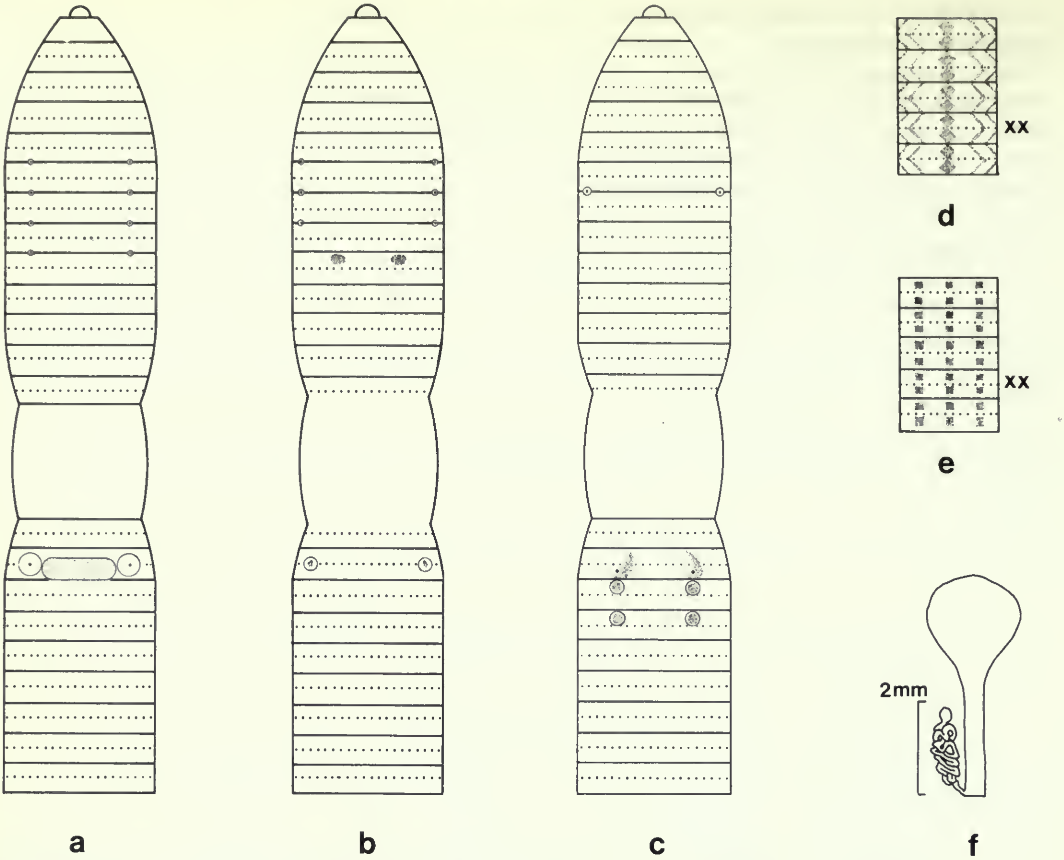

Fig. 30 Anterior ventral surface, diagnostic characters. (a) *Planapheretima arboricola*; (b) *P. continens*; (c) *P. sera* sp. nov. Dorsal pigmentation. (d) *P. lacertina*; (e) *P. tenebrica*. Spermatheca. (f) *P. sera* sp. nov.

Holandric, testes sacs paired, those of *x* extending to the dorsal line, those of *xi* smaller, seminal vesicles small in *xi* and *xii*. Spermathecae (Fig. 27i) paired in *vi–viii* or occasionally *v–vii*.

Description after Chen (1946).

DISTRIBUTION. Szechwan, China.

RECORDS. 2 specimens Mt Omei, Szechwan, China (types of *continens*). 2 specimens under moss, Changking, Szechwan, China (*continens*: Chen, 1946).

Planapheretima arboricola (Rosa, 1890)

Perionyx arboricola Rosa, 1890 : 119; Beddard, 1895 : 438; Michaelsen, 1900 : 209; Michaelsen, 1903*b* : 89; Stephenson, 1923 : 326; Gates, 1936*a* : 465; Gates, 1961 : 57; Gates, 1972*a* : 141.
Pheretima arboricola Gates, 1936*a* : 399; Gates, 1972*a* : 169.
Planapheretima arboricola: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Planapheretima* with multiple intestinal caeca; spermathecal pores in furrows 5/6/7/8/9.

DESCRIPTION. *External characters*. Length *c*. 70 mm, diameter *c*. 5 mm. *C*. 110 segments. Body depressed, creeping sole on postclitellar segments becoming narrower posteriorly. Colouration; dark green or reddish dorsally, pale yellow ventrally, clitellum violet grey. Clitellum *xiv–xvi*. First dorsal pore ? 5/6 or 11/12. Setae *c*. 72 on *vii*, *c*. 60 on *xx*. Setal ring crowded ventrally, 7*ab*=*yz*.

Male pores on large hemispherical porophores *c.* 0·18 body circumference apart. Female pore single. Spermathecal pores small paired, intersegmental in 5/6/7/8/9, *c.* 0·26 body circumference apart.

Genital markings (Fig. 30a) single, median, *xviii.*

Internal characters. Anterior septa delicate, 8/9/10 absent. Intestine begins in *xv* with paired, lateral multiple caeca originating in *xxvii*, details of intestinal wall not recorded. Lateral hearts in *x–xiii.*

Holandric, testes sacs single, ventral in *x* and *xi*, seminal vesicles large in *xi* and *xii*. Spermathecae (Fig. 27j) paired in *vi–ix.*

Fig. 30a is an interpretation of the genital field based on the written description of Gates (1936). The holotype lacks genital markings.

DISTRIBUTION. Burma.

REMARKS. The holotype of *Pheretima arboricola* Gates (1936) was recorded as being in the Museo Civico di Storia Naturale 'Giacomo Doria', Genoa (Reynolds & Cook, 1976). However, the specimen (44017) proved to be the holotype of *Perionyx arboricola* Rosa (1890) which had originally been reported as having a gizzard in *v* and a holonephric excretory system. On re-examination it was found that Rosa's description was inaccurate since the gizzard is in *viii* and the excretory system is micronephric, characters of the *Pheretima* group. Unfortunately the intestine was poorly preserved so preventing the recognition of any intestinal structures important for specific diagnosis within *Planapheretima.* It is assumed that caeca were once present in the holotype since Gates (1936) described an otherwise identical earthworm, destroyed in Burma between 1942 and 1945, which possessed these structures. [The paratype of *Perionyx arboricola*, Berlin 2270 (Reynolds & Cook, 1976 : 71) is a juvenile *Perionyx* of uncertain specific identity.]

MATERIAL EXAMINED. 1C Lacking anterior intestine and most of oesophagus, on trees, especially in the axils of leaves, Cobapo, Mt Carin, Cheba or Biapo district, Burma, *coll* L Fea; Genoa 44017 (holotype of *arboricola* Rosa, 1890).

OTHER RECORDS. 1C Toungoo district, Burma (holotype of *arboricola* Gates, 1936).

Planapheretima lacertina (Chen, 1946)

Pheretima lacertina Chen, 1946 : 109.
Planapheretima Sims & Easton, 1972 : 233.

DIAGNOSIS. *Planapheretima* with rudimentary caeca; spermathecal pores in furrows 5/6/7/8/9.

DESCRIPTION. *External characters.* Length *c.* 81–82 mm, diameter 4–4·5 mm. 90–100 segments. Body depressed and concave ventrally, creeping sole not recorded. Colouration; dark chestnut or brownish black pattern (Fig. 30d) on a bluish background. Clitellum *xiv–xvi.* First dorsal pore 10/11. Setae, *c.* 72 on *iii*, *c.* 78 on *vi*, *c.* 81 on *ix*, *c.* 72 on *xxv*, setal ring crowded ventrally (3–4$ab = yz$) dorsal and ventral gaps not recorded.

Male pores in large glandular, circular depressions *c.* 0·33 body circumference apart. Female pore(s) not recorded. Spermathecal pores small in 5/6/7/8, separation uncertain [either 0·33 or 0·44 body circumference apart (see remarks under *bambophila* species-group)].

Genital markings, none recorded.

Internal characters. All anterior septa present and delicate except for 6/7–8/9 which are slightly thickened. Intestine begins in *xv* with paired rudimentary lateral caeca restricted to *xxvi*, intestinal wall posterioriad to caeca glandular. Disposition of lateral hearts not recorded.

Holandric, testes sacs single in *x* and *xi*, seminal vesicles large in *xi*, those of *xii* extending posteriorly to *xiv*. Spermathecae (Fig. 27k) paired in *vi–ix*.

Description after Chen (1946).

DISTRIBUTION. Szechwan, China.

RECORDS. 2 specimens, among moss on bark of trees, Mt King-Fu, Szechwan, China, 2000 ft (types of *lacertina*).

Planapheretima tenebrica (Chen, 1946)

Pheretima tenebrica Chen, 1946 : 93.
Planapheretima tenebrica: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Planapheretima* with an intestine lacking caeca but with thickened walls in *xxvi–xxxvi*; spermathecal pores in furrows 5/6/7/8/9.

DESCRIPTION. *External characters.* Length 35–60 mm, diameter 2–2·8 mm. *C.* 82 segments. Shape of body and creeping sole not recorded. Colouration; three longitudinal reddish brown dorsal stripes (Fig. 30e) on a chocolate-coloured background, clitellum dark chocolate to brick red. Clitellum *xiv–xvi*, encroaching onto *xiii* and *xvii*. First dorsal pore 9/10. Setae, 46–50 on *iii*, 52–60 on *ix*, 50–52 on *xix* and *xxv*, setal ring crowded ventrally with dorsal and slight ventral gaps (*aa*=1–1·1*ab*; *zz*=2–2·5*yz*).

Male pores on circular porophores, separation uncertain [either 0·20 or 0·33 body circumference apart (see remarks under *bambophila* species-group)]. Female pore(s) not recorded. Spermathecal pores small in 5/6/7/8/9, separation uncertain (either 0·20 or 0·33 body circumference apart).

Genital markings, none recorded.

Internal characters. All anterior septa present and delicate. Intestine begins in *xv*, caeca absent, intestinal walls of *xxvi–xxxvi* thickened. Disposition of lateral hearts not recorded.

Holandric, testes sacs of *x* paired but meeting ventrally, that of *xi* single ventral, seminal vesicles large in *xi* and *xii* extending posteriorly 5–7 segments. Spermathecae (Fig. 27l) paired in *vi–ix*.

Description after Chen (1946).

DISTRIBUTION. Szechwan, China.

RECORDS. 9 specimens, Mt Omei, Szechwan, China, 5000 ft (holotype and paratypes of *tenebrica*); 1 specimen in sandy ground under stone near creek, Nan-Chuan-Hsein, Szechwan, China (paratype of *tenebrica*).

Planapheretima bambophila (Chen, 1946)

Pheretima bambophila Chen, 1946 : 86.
Planapheretima bambophila: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Planapheretima* with an intestine lacking caeca but with thickened walls in *xxii–xxxviii*; spermathecal pores in furrows 7/8/9.

DESCRIPTION. *External characters.* Length 40–55 mm, diameter 3–4 mm. 88–94 segments. Body depressed with a glandular creeping sole on *viii–ix* and from the male pores to the posterior end of the body. Colouration; purplish brown dorsally, pale ventrally. Clitellum *xiv–xvi*. First dorsal pore 10/11. Setae, *c.* 84 on *x*, *c.* 54 on *xix*, *c.* 52 on *xxv*, *c.* 44 on *xl*, setal ring crowded ventrally, especially on the creeping sole (*ab*=0·6*yz* on *xix*).

Male pores simple within the creeping sole, *c.* 0·25 body circumference apart. Female pore single. Spermathecal pores small in 7/8/9, *c.* 0·25 body circumference apart.

Genital markings, none recorded.

Internal characters. All anterior septa present and delicate; intestine begins in *xv*, caeca absent but walls thickened and forming pouches in *xxii-xxix* and less conspicuously in *xxx–xxxviii*. Disposition of lateral hearts not recorded.

Holandric, testes sacs small single ventral in *x* and *xi*, seminal large in *xi* and *xii*, extending anteriorly to *ix* and posteriorly to *xvii*. Spermathecae (Fig. 27m) paired in *viii* and *ix*.

Description after Chen (1946).

DISTRIBUTION. Szechwan, China.

RECORDS. 3 specimens on bushy bamboos, Kiu-Lac-Tung, Mt Omei, Szechwan, China (types of *bambophila*).

METAPHERETIMA Michaelsen, 1928

Perichaeta (part): Beddard, 1895 : 388.
Amynthas (part): Beddard, 1900*a* : 612.

Pheretima (part): Michaelsen, 1900 : 234.
Pheretima (*Pheretima*) (part): Michaelsen, 1928*a* : 8.
Pheretima (*Metapheretima*) (part) Michaelsen, 1928*a* : 8.
Metapheretima (part): Sims & Easton, 1972 : 205, 233.
Pheretima (*Polypheretima*) (part): Michaelsen, 1934*b* : 15.
Ephemitra Sims & Easton, 1972 : 203, 232.

TYPE SPECIES. *Perichaeta neoguinensis* Michaelsen, 1892, original designation.

DIAGNOSIS. Megascolecidae with an oesophageal gizzard in *viii*, intestinal caeca and gizzards absent. Body cylindrical, setae never excessively crowded ventrally, creeping sole absent. Male pores lacking porophores, occasionally on slim penes which may be within copulatory pouches. Crescentic genital markings associated with the male pores on mature individuals of most species. Spermathecal pores small or large, spermathecal diverticula variable in structure and origin.

DESCRIPTION. Body cylindrical, creeping sole absent. Clitellum annular, usually restricted to three segments (*xiv–xvi*), rarely extending over more (*xiii, xvii*). First dorsal pore between 8/9 and 13/14. Setae perichaetine, never excessively crowded ventrally, dorsal and ventral gaps small ($aa = 1–2ab$, $zz = 1{\cdot}2yz$). Lateral hearts in *x–xii* and sometimes *xiii*.

Oesophagus with a well-developed gizzard in *viii* and occasionally a pair of dorsal pouches in *x–xi*, calciferous glands absent. Intestine usually begins in *xv* or *xvi* but may begin more posteriorly in *xx*; simple, lacking caeca, gizzards and glandular walls.

Usually holandric, occasionally metandric, rarely proandric. The testes of each segment are enclosed in a single or paired sacs which are usually small and discrete, occasionally enclosing the anterior seminal vesicles. One pair of seminal vesicles in the segment directly posterior to each pair of testes. Prostates racemose. Paired, combined male and prostatic pores on the ventral surface of *xviii* in the setal ring. Male pores occasionally on slim penes, often within copulatory pouches; porophores absent.

Ovaries free in *xiii*. Oviducts lead to single or closely paired, midventral, equatorial pore(s) on *xiv*. Spermathecae differentiated into duct and ampulla, diverticula variable in structure and origin. Spermathecae usually arranged in pairs, infrequently in paired batteries of up to 8 spermathecae; in one to five adjacent segments between *v* and *ix*. Spermathecal pores small or slit-like, always intersegmental.

Genital markings of the discrete type or annular ridges; diffuse markings absent. In most species crescentic markings are closely associated with the male pores. In those species where they are absent the male pore may be surrounded by a pigmented annulus. The genital markings are usually arranged in pairs, they are never random or numerous (cf. *Polypheretima bifaria* and *patae* species-groups). The glandular tissue associated with the genital markings is restricted to the body wall and never invades the coelom.

DISTRIBUTION. (Fig. 7.) North and south east New Guinea, New Britain, Lombok. Species may be indigenous in the Carolines, Solomon Islands and New Hebrides.

NUMERICAL STUDIES. The taxa of the genus *Metapheretima* listed in Table 1 (7–36) were investigated numerically utilizing characters 3–29 in Table 2. Distributional data (characters 1 and 2) were not employed since the majority of taxa of *Metapheretima* are known only from New Guinea and the autochthony or otherwise of populations from elsewhere is uncertain.

The configuration of the taxa with the first and second vectors of the principal co-ordinates analysis as axes to which the MST with graded linkages has been added is shown in Fig. 31. Three divisions, indicated by circular, triangular and square symbols, may be recognized together with an isolated taxon *jocchana* (36) indicated by a star-shaped symbol.

Unlike the divisions recognized within the other acaecate genera reviewed above, those of *Metapheretima* form more diffuse configurations. Most of the taxa with simple male pores are accommodated in Division I. Species of this division usually have four to five thecal segments, ectal spermathecal diverticula and the male pores never possess annular ridges.

Taxa with male pores on penes are assigned to Divisions II and III; those with several thecal segments and ectal spermathecal diverticula form Division II while those with one or two thecal

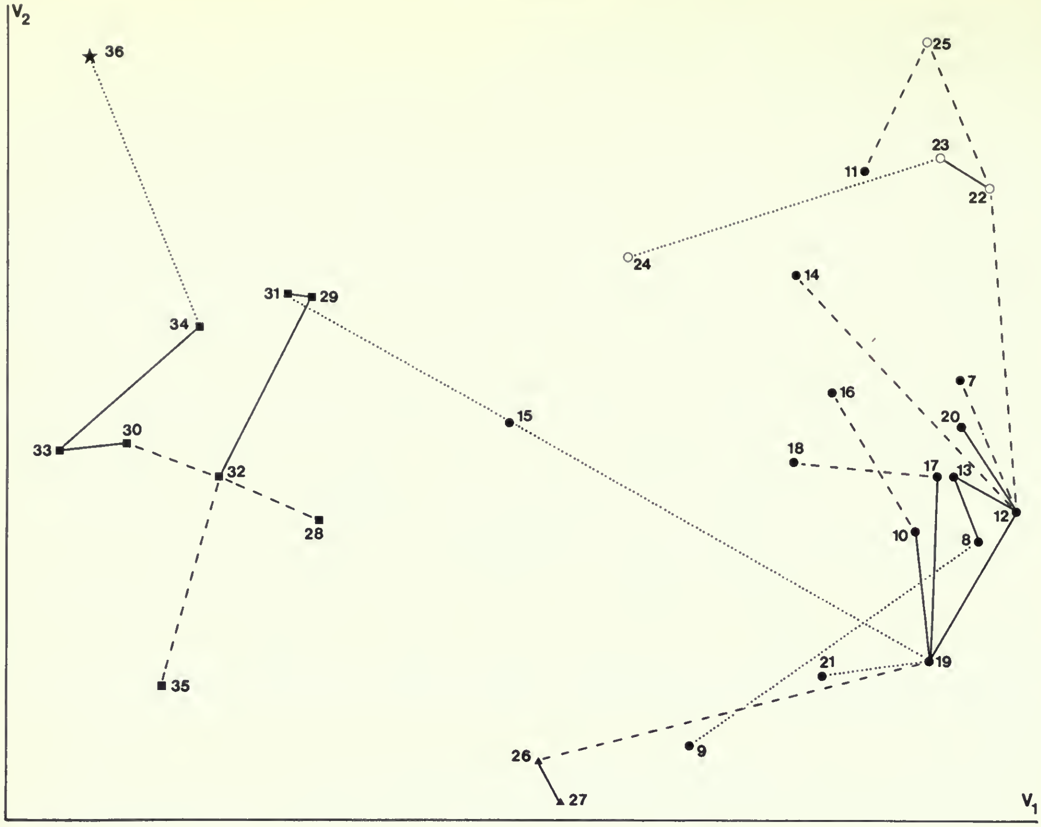

Fig. 31 Principal co-ordinates analysis of 30 species here assigned to *Metapheretima* (7–36 of Table 1): the configuration of species with the vectors corresponding to the first and second latent roots. The linkages of the added MST are graded to indicate percentage similarities; ——, +95%; - - - - -, 90–95%; · · · · ·, −90%. Three major assemblages and an isolated species are recognized:

Division I – circular symbols (closed circles – *bulmeri* species-group, open circles – *neoguinensis* species-group).

Division II – triangular symbols (*durendali* species-group).

Division III – square symbols (*oinakensis* species-group).

Metapheretima jocchana – star-shaped symbol.

segments and ental spermathecal diverticula form Division III. Annular ridges are often associated with the male pores of taxa included in Division III. The isolated taxon *jocchana* (36) has simple male pores encircled by annular ridges, a single thecal segment and numerous ental diverticula on the spermathecae.

Division I comprises two clusters, the members of each are denoted by closed or open circular symbols. Species 11 (*pallens*) has been included in the cluster with closed circular symbols because five of its six nearest neighbours belong to this group although it is linked by the MST to the other cluster. Species forming the two clusters may be distinguished by the form of the spermathecal diverticula. The cluster formed by closed circular symbols comprise taxa with simple diverticula, the *bulmeri* species-group; the other cluster with open circular symbols consist of the species with multiocular spermathecal diverticula, the *neoguinensis* species-group. The inclusion of the species *sembaluensis* (15) in Division I needs comment. Although its nearest neighbours belong to Division III (square symbols) it is assigned to Division I (circular symbols) since it lies intermediately between the two divisions and possesses the marker characters of Division I.

The two species of Division II form the *durendali* species-group while those of Division III comprise the *oinakensis* species-group.

Table 12 Phenetic classification and checklist of the genus *Metapheretima*

Division I	*bulmeri* species-group	*arensi* (7)
		bulmeri (8)
		carolinensis (9)
		elrondi (10)
		lindiae
		pallens (11)
		pickfordi (12)
		queribunda (13)
		quinqueremis (14)
		sembaluensis (15)
		sentanensis (16)
		simsi (17)
		sola (18)
		speiseri (19)
		triciae (20)
		trukensis (21)
	neoguinensis species-group	*deirdriae*
		loriae (22)
		neoguinensis (23)
		septocta (24)
		sucklingensis (25)
Division II	*durendali* species-group	*durendali* (26)
		excalaberi (26)
Division III	*oinakensis* species-group	*andurili* (28)
		dorii (29)
		glamdringi (30)
		kilii (31)
		oinakensis (32)
		orcrista (33)
		parmata (34)
		stingi (35)
		tawarinensis
		jocchana (36)

Numbers in parentheses indicate taxa assessed in numerical studies (see Figs 6 and 31).

Metandry or Holandry appears to be of little taxonomic value in the recognition of the species-groups within the genus *Metapheretima*. The importance of the number and distribution of testes in members of this genus is in contrast to the numerical study of the genus *Polypheretima* where these characters proved to be valuable indicators.

A summary of the phenetic classification based on this numerical study is given in Table 12.

Key to the species of the genus *Metapheretima*

1	First spermathecal pores in furrow 4/5	2
	First spermathecal pores in furrow 5/6	12
	First spermathecal pores in furrow 6/7	19
	First spermathecal pores in furrow 7/8	21
2	Two thecal segments	3
	Four thecal segments	***durendali*** (part) (p. 105)
	Five thecal segments	4
3	Holandric; genital markings as Fig. 42a	***excalaberi*** (p. 104)
	Metandric; genital markings as Fig. 34a	***arensi*** (p. 83)

4(2)	Proandric or holandric	5
	Metandric	8
5	Setal numbers very low (less than 40 on *vii* even in large specimens) polythecal	***bulmeri*** (p. 84)
	Setal numbers intermediate (bithecal)	6
	Setal numbers very high (more than 100 on *vii* even in small specimens) bithecal	***sentanensis*** (p. 88)
6	Preclitellar genital markings single, spermathecal pores *c.* 0·50 body circumference apart	***pickfordi***[1] (p. 91)
	Preclitellar genital markings paired, spermathecal pores 0·26–0·40 body circumference apart	7
7	Testes in *x* only	***queribunda*** (p. 90)
	Testes in *x* and *xi*	***speiseri*** (part) (p. 92)
8(4)	Spermathecal diverticulum simple	9
	Spermathecal diverticula multilocular	***loriae*** (p. 99)
9	Spermathecal diverticulum short and ental in origin	***quinquerimis*** (p. 85)
	Spermathecal diverticulum long and ectal in origin	10
10	Bithecal; preclitellar genital markings single or absent	11
	Polythecal; preclitellar genital markings paired	***lindae*** (p. 89)
11	Postclitellar genital markings single (preclitellar genital markings absent)	***simsi*** (p. 87)
	Postclitellar genital markings paired (preclitellar genital markings single)	***pickfordi***[1] (p. 91)
12(1)	One or two thecal segments	***andurili*** (p. 109)
	Three thecal segments	13
	Four thecal segments	15
13	Spermathecal pores numerous on dorsal surface	***carolinensis*** (p. 96)
	Spermathecal pores paired on ventral surface	14
14	Male pores simple: genital markings as Fig. 39a	***trukensis*** (p. 96)
	Male pores on penes within copulatory pouches; genital markings as Fig. 42b	***durendali*** (part) (p. 105)
15(2)	Holandric	16
	Metandric	17
16	Preclitellar genital markings on *vii–ix*	***speiseri*** (part) (p. 92)
	Preclitellar genital markings on *ix–xi*	***elrondi*** (p. 93)
17(5)	Spermathecal diverticulum simple	18
	Spermathecal diverticulum multilocular	***neoguinensis*** (p. 99)
18	Setal numbers low (less than 40 on *vii* even in large specimens)	***sola*** (p. 93)
	Setal numbers high (more than 100 on *vii* even in small specimens)	***triciae*** (p. 94)
19(1)	One or two thecal segments	***durendali*** (part) (p. 105)
	Three thecal segments	20
20	Spermathecal diverticulum simple	***speiseri*** (part) (p. 92)
	Spermathecal diverticulum multilocular	***sucklingensis*** (p. 102)
21(1)	One thecal segment	22
	Two thecal segments	26
22	Spermathecal diverticulum simple	23
	Spermathecal diverticulum multilocular	***septocta*** (p. 103)
	Spermathecal diverticulum numerous (Fig. 33p)	***jocchana*** (p. 113)
23	Proandric	***glamdringi*** (p. 113)
	Holandric	24
	Metandric	25
24	Postclitellar genital field as Fig. 43a	***tawarinensis*** (p. 106)
	Postclitellar genital field as Fig. 44b	***stingi*** (p. 109)
	Postclitellar genital field as Fig. 44c	***oinakensis*** (p. 111)
	Postclitellar genital field as Fig. 45a	***orcrista*** (p. 112)
	Postclitellar genital field as Fig. 45b	***parmata*** (p. 112)
25(23)	Genital markings as Fig. 43b (spermathecal pores *c.* 0·20 body circumference apart)	***kilii*** (p. 107)
	Genital markings as Fig. 43c (spermathecal pores *c.* 0·37 body circumference apart)	***dorii*** (p. 108)
26(21)	Holandric	***sembaluensis*** (p. 98)
	Metandric	27

27	Spermathecal diverticulum simple	*pallens* (p. 98)
	Spermathecal diverticulum multilocular	*deirdrae* (p. 102)

[1] The unique holotype of *pickfordi* is damaged and may be holandric or metandric, it has therefore been keyed out twice to allow for either condition.

Metapheretima bulmeri species-group

DIAGNOSIS. *Metapheretima* with simple male pores lacking associated glandular ridges. Spermathecal diverticula simple.

SPECIES INCLUDED. *arensi*, *bulmeri*, *carolinensis*, *elrondi*, *lindiae*, *pallens*, *pickfordi*, *queribunda*, *quinqueremis*, *sembaluensis*, *sentanensis*, *simsi*, *sola*, *speiseri*, *triciae*, *trukensis*.

DISTRIBUTION. Species occur in all parts of the generic range.

REMARKS. The *bulmeri* species-group includes all the species of the genus *Metapheretima* possessing simple male pores with the exception of those which additionally have multilocular or numerous spermathecal diverticula. The latter are assigned to the *neoguinensis* species-group and to *jocchana* respectively. The results of the numerical studies failed to reveal any subassemblages with high percentage similarities indicative of subdivisions within the *bulmeri* species-group.

The inter-relationships of the species recorded from the New Hebrides and Solomon Islands are far from certain. Although each taxon is treated here as a separate species, it is probable that when further material becomes available they will be found to be conspecific.

Several of the species included in this group have the oesophagus modified in *x* and/or *xi* to form dorsal or dorsolateral pouches. Considerable variation in the degree of development of these structures may be encountered within individuals of a species. The presence of these pouches was utilized as a diagnostic generic character (*Ephemitra* Sims & Easton, 1972). The development of oesophageal pouches among the species of this group may to some extent be functionally correlated with the development of metandry since the enlargement of the oesophagus in *x* limits the space available for testes and testes sacs.

Marker characters of the species included in the *bulmeri* species-group are given in Table 13.

Metapheretima arensi (Ude, 1932)

Pheretima (*Metapheretima*) *arensi* Ude, 1932 : 168.
Metapheretima arensi: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one third of the body circumference apart in furrows 4/5/6. Metandric.

DESCRIPTION. *External characters*. Length 90–110 mm, diameter, 3·5–4 mm. 125–154 segments. Clitellum *xiv–xvi*. First dorsal pore 11/12. Setae, 140–150 on *vii*, 75–95 on *xx*, setal ring regular with ventral gaps ($aa = 2ab = 2yz = 2zz$).

Male pore simple, *c*. 0·20 body circumference apart. Female pores paired. Spermathecal pores small, paired in 4/5/6, *c*. 0·30 body circumference apart.

Genital markings (Fig. 34a) single, median presetal on *ix* and *x*, paired, presetal in line with the male pores on *xvii* and *xix*.

Internal characters. Septa 5/6/7/8 thickened, 8/9 membranous, 9/10 absent, 10/11 thickened. Oesophagus with small dorsal pouches in *x–xii*. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Metandric, testes sacs small, paired ventral in *xi*, seminal vesicles large, extending to the dorsal line in *xii*. Spermathecae (Fig. 32a) paired in *v* and *vi*.

DISTRIBUTION. New Britain.

MATERIAL EXAMINED. *Previously reported*. 3C, 1A Mejin bay, New Britain; Hamburg v3429 (syntypes of *arensi*) 2 other specimens from this series have been re-identified as *Pithemera pacifica* (Beddard, 1899); Hamburg v10032. 1A Aid river, New Britain; Hamburg v3458 (syntype of *arensi*). 1C Lieblide Island, New Britain; Hamburg v10031 (syntype of *arensi*).

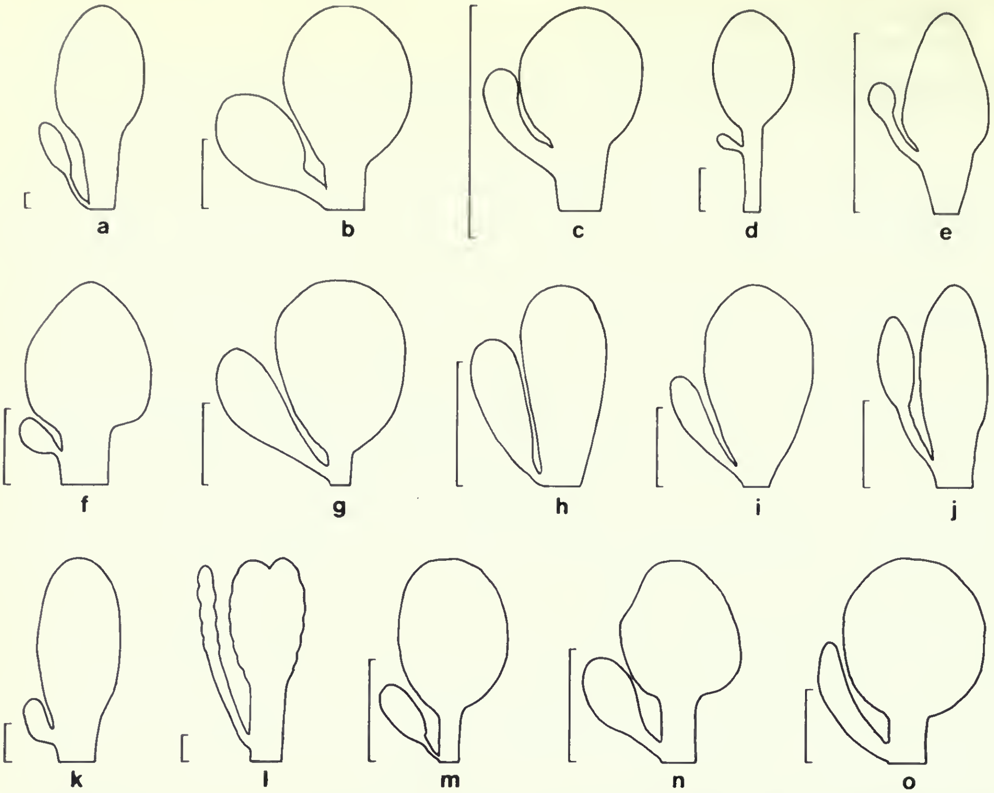

Fig. 32 Spermathecae. (a) *Metapheretima arensi*; (b) *M. bulmeri*; (c) *M. lindiae* sp. nov.; (d) *M. quinqueremis* sp. nov.; (e) *M. simsi* sp. nov.; (f) *M. sentanensis*; (g) *M. queribunda*; (h) *M, speiseri*; (i) *M. elrondi* sp. nov.; (j) *M. sola* sp. nov.; (k) *M. triciae* sp. nov.; (l) *M. trukensis*; (m) *M. carolinensis*; (n) *M. sembaluensis*; (o) *M. pallens*. All scales 0·5 mm.

New record. 1C Tu Island, New Britain. This specimen was removed from a series of *Pithemera sedgewicki typica*: Ude, 1932; Hamburg v3470.

Metapheretima bulmeri (Gates, 1970)

Pheretima bulmeri Gates, 1970*b* : 386.
Metapheretima bulmeri: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores; numerous spermathecal pores in paired batteries about one quarter of the body circumference apart in furrows 4/5/6/7/8/9. Holandric. Setal numbers low (cf. *kinabaluensis* Fig. 2) diverticula simple, ectal.

DESCRIPTION. *External characters.* Length 200–340 mm, diameter 10–14 mm. 105–129 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, *c.* 42 on *vii*, *c.* 50 on *xx*, setal ring regular with dorsal gaps ($aa = ab = yz = 0{\cdot}5zz$).

Male pores simple, *c.* 0·20 body circumference apart. Female pore single. Spermathecal pores small, numerous in paired batteries of up to 7 pores in 4/5/6/7/8/9, *c.* 0·28 circumference apart.

Genital markings (Fig. 34b), only those diagnostic of the genus.

Internal characters. Septa 4/5–7/8 membranous, 8/9/10 absent, 10/11 membranous, 11/12–14/15 slightly thickened. Oseophagus unmodified. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Holandric, testes sacs small, paired in *x* and *xi*, seminal vesicles extending to the dorsal line in *xi* and *xii*. Pseudoseminal vesicles in *xiii*. Spermathecae (Fig. 32b), numerous, arranged in paired batteries of up to 7 spermatheca in *v–ix*.

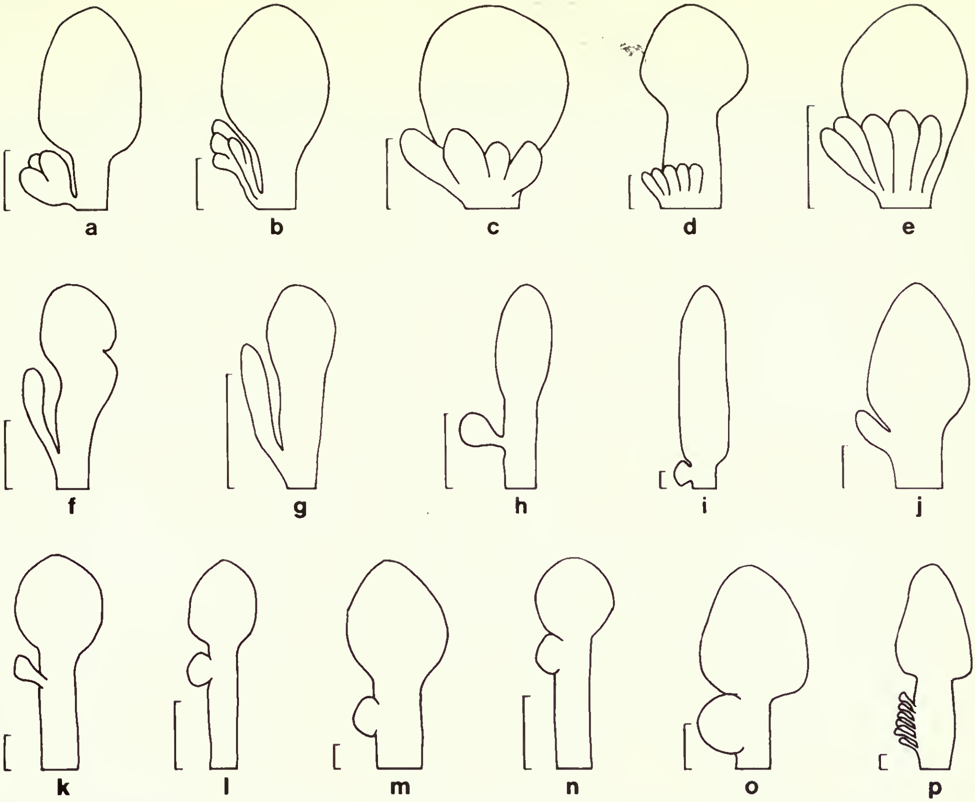

Fig. 33 Spermathecae. (a) *Metapheretima loriae*; (b) *M. neoguinensis*; (c) *M. sucklingensis* sp. nov.; (d) *M. dierdrae* sp. nov.; (e) *M. septocta* sp. nov.; (f) *M. excalaberi* sp. nov.; (g) *M. durendali* sp. nov.; (h) *M. tawarinensis*; (i) *M. kilii* sp. nov.; (j) *M. dorii* sp. nov.; (k) *M. andurili* sp. nov.; (l) *M. stingi* sp. nov.; (m) *M. oinakensis*; (n) *M. orcrista* sp. nov.; (o) *M. glamdringi* sp. nov.; (p) *M. jocchana*. All scales 0·5 mm.

DISTRIBUTION. North east New Guinea.

MATERIAL EXAMINED. *Previously reported.* 2C Schrader range, Papua New Guinea; Sydney v4259 (syntypes of *bulmeri*). I am indebted to Dr B. G. M. Jamieson, University of Queensland, for examining the types and for making drawings on which the figures of the genital markings and spermathecae are based.
New record. 1C, 1A Schrader range, Papua New Guinea; BMNH 1976.2.1–2.

Metapheretima quinqueremis sp. nov.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one fifth of the body circumference apart in furrows 4/5/6/7/8/9. Metandric. Setal numbers intermediate (cf. *elongata*, Fig. 2). Spermathecal diverticula simple, ectal.

DESCRIPTION. *External characters.* Length 86–122 mm, diameter 4–5 mm. 73–97 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, 40–44 on *vii*, 41–44 on *xx*, setal ring regular with dorsal and ventral gaps ($aa = 1{\cdot}5ab = 1{\cdot}5yz = zz$).

Male pores simple *c.* 0·20 body circumference apart. Female pores paired. Spermathecal pores small, paired, in 4/5/6/7/8/9, *c.* 0·20 body circumference apart.

Genital markings (Fig. 35a), large, paired, presetal slightly median to the spermathecal pores on *vi–ix*, in line with the male pores on *xvii*, *xix–xx*.

Table 13 Marker characters of the members of the *Metapheretima bulmeri* species-group

Species	Spermathecal furrows	Separation of spermathecal pores	Setal density[1]	Genital markings (S = single, P = paired) Preclitellar	Genital markings (S = single, P = paired) Postclitellar	Testes (P = proandric H = holandric M = metandric)	Distribution
arensi	4/5/6	0·30	h	S, *ix*, *x*	P, *xvii*, *xix*	M	New Britain
bulmeri	4/5/6/7/8/9	0·28 (polythecal)	l	–	–	H	New Guinea
quinqueremis	4/5/6/7/8/9	0·20	i	P, *vi–ix*	P, *xvii*, *xix–xx*	M	New Guinea
simsi	4/5/6/7/8/9	0·35	i	–	S, *xvii–xx*	M	New Guinea
sentanensis	4/5/6/7/8/9	0·20–0·29	h	P, *viii–x*	P, *xvii*, *xix–xxv*	H	New Guinea
lindiae	4/5/6/7/8/9	0·23 (polythecal)	h	P, *ix*	P, *xvii*, *xix–xxiii*	M	New Guinea
queribunda	4/5/6/7/8/9	0·35	h	P, *vi–ix*	P, *xvii*, *xx–xxii*	P[2]	Solomon Is.
pickfordi	4/5/6/7/8/9	0·50	h	S, *vii–ix*	P, *xvii*, *xix–xxiii*	? M	Solomon Is.
speiseri	4/5/6/7/8/9 5/6/7/8/9 or 6/7/8/9	0·26–0·40	i	P, *vii–ix*	P, *xvii*, *xix–xx*	H	New Hebrides
elrondi	5/6/7/8/9	0·25	h	P, *ix–xi*	P, *xvii*, *xix–xxiii*	H	New Guinea
sola	5/6/7/8/9	0·08	l	P, *vi–ix*	P, *xvii*, *xix–xxi*	M	New Guinea
triciae	5/6/7/8/9	0·20–0·26	h	P, *vii–x*	P, *xvi–xxi*	M	New Guinea
trukensis	5/6/7/8	0·10	l	–	P, *xvii*, *xix–xxi*	H	Caroline Is.
carolinensis	5/6/7/8	0·90 (polythecal)	i	–	–	H	Caroline Is.
sembaluensis	7/8/9	0·20	i	P, *viii–ix*	P/S *xvii–xx*	H	Lombok
pallens	7/8/9	0·31	h	P, *viii–x*	P, *xvii*, *xx–xxii*	M	New Guinea

[1] For details of setal densities see Fig. 2. Low = cf. *kinabaluensis*, intermediate = cf. *elongata*, high = cf. *sentanensis*.
[2] Although proandric, *queribunda* has testes sacs in *xi* as well as *x*.

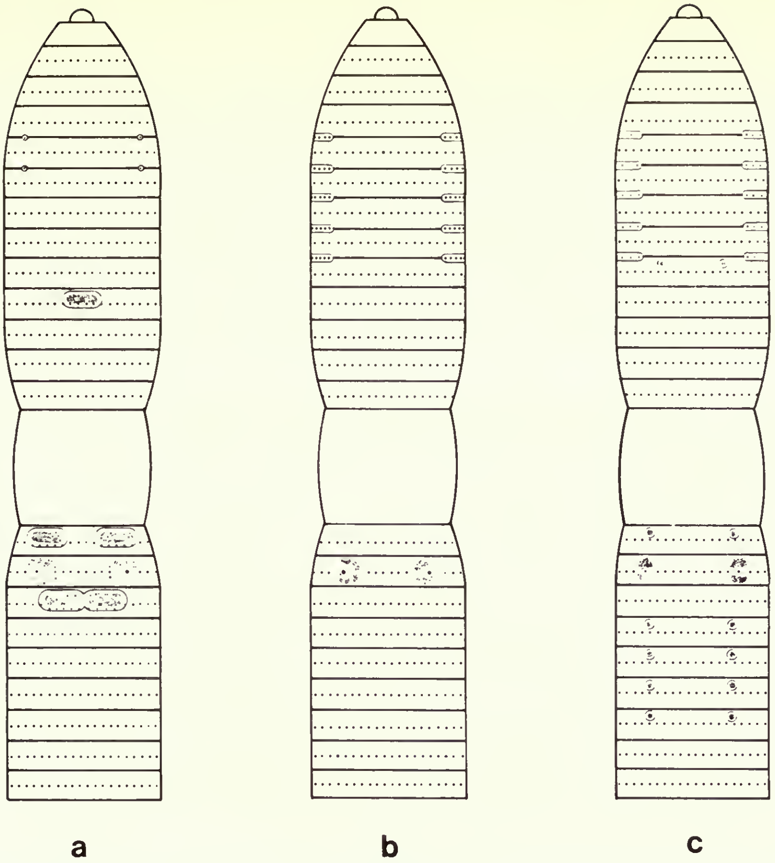

Fig. 34 Anterior ventral surface, diagnostic characters. (a) *Metapheretima arensi*; (b) *M. bulmeri*; (c) *M. lindiae* sp. nov.

Internal characters. Septa 4/5–12/13 present and membranous. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs small, paired, ventral in *xi*, seminal vesicles large, extending to the dorsal line in *xii*. Pseudoseminal vesicles prominent in *xiv*. Spermathecae (Fig. 32d) paired in *v–ix*.

DISTRIBUTION. South east New Guinea.

MATERIAL EXAMINED. 25C, 1A Mt Suckling, Papua New Guinea, 9° 46′ S, 149° 00′ E, *coll* W H Ewer 1972; BMNH 1976.4.30–54 (syntypes of *quinqueremis*). 1C Gentle ridge, Bismarck range, Eastern Highland district, Papua New Guinea, 5° 57′ S, 145° 15′ E, 2500 m, *coll* D R Kershaw 14 Jul 1971; BMNH 1976.5.116.

Metapheretima simsi sp. nov.

DIAGNOSIS. *Metapheretima* with simple male pores; spermathecal pores about one third of the body circumference apart in furrows 4/5/6/7/8/9. Metandric. Setal numbers intermediate (cf. *elongata*, Fig. 2). Postclitellar genital markings single, median, presetal. Spermathecal diverticula simple, ectal.

DESCRIPTION. *External characters.* Length *c.* 36 mm, diameter *c.* 1·5 mm. *C.* 118 segments. Clitellum *xiv–xvi*. First dorsal pore not detectable in preclitellar furrows. Setae, *c.* 41 on *vii*, *c.* 30 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores simple, *c.* 0·24 body circumference apart. Female pores paired. Spermathecal pores small, paired, in 4/5/6/7/8/9, *c.* 0·35 body circumference apart.

Genital markings (Fig. 35b) oval, single, presetal, median on *xvii–xx*.

Internal characters. Septa 6/7/8 thickened, 8/9–13/14 membranous. Oesophagus simple. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs large, paired with dorsal link in *xi*, seminal vesicles extending to the lateral line in *xii*. Spermathecae (Fig. 32e) paired in *v–ix*.

DISTRIBUTION. New Guinea.

REMARKS. The possession of single median postclitellar genital markings distinguishes this species from all other members of the genus *Metapheretima* with five thecal segments.

MATERIAL EXAMINED. 1C Woitape, Goilala, Papua New Guinea, 8° 22′ S, 147° 03′ E, altitude 1500 m, *coll* Griffiths 2 Jul 1972; BMNH 1976.10.19 (holotype of *simsi*).

Metapheretima sentanensis (Cognetti, 1911)

Pheretima sentanensis Cognetti, 1911 : 5; Cognetti, 1912 : 551.
Ephemitra sentanensis: Sims & Easton, 1972 : 181, 204, 232.
Pheretima myritchasta (sic) Cognetti, 1911 : 4.
Pheretima myriochaeta: Cognetti, 1912 : 549.
Ephemitra myriochaeta: Sims & Easton, 1972 : 181, 232.
Pheretima ardita Cognetti, 1914 : 353.
Pheretima (*Pheretima*) *ardita*: Ude, 1932 : 145.
Ephemitra ardita: Sims & Easton, 1972 : 180, 232.
Pheretima tamiensis Ude, 1924 : 84.
Pheretima (*Pheretima*) *tamiensis*: Ude, 1932 : 136.
Metapheretima tamiensis: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one quarter of the body circumference apart in furrows 4/5/6/7/8/9. Holandric. Setal numbers high (Fig. 2). Spermathecal diverticula simple, ectal.

DESCRIPTION. *External characters.* Length 25–145 mm, diameter 1·5–5 mm. 90–212 segments. Clitellum *xiv–xvi*. First dorsal pore occasionally 8/9/10 but usually 12/13. Setae, 100–300 on *vii*, 50–128 on *xx*, setal ring regular but occasionally with displaced setae forming double rings (*aa*=*ab*=*yz*=*zz*).

Male pores simple, *c.* 0·20–0·27 body circumference apart. Female pore single, rarely paired. Spermathecal pores small, paired, 4/5/6/7/8/9, *c.* 0·20–0·29 body circumference apart.

Genital markings (Fig. 35c, d) paired, median to the line of the spermathecal pores, presetal on *viii–x* and occasionally postsetal on *viii* and *ix*, in line with or slightly median to the male pores, presetal on *xvii*, *xix–xxv*.

Internal characters. Septa 5/6/7/8 thickened, 8/9 membranous, 9/10 membranous or absent, 10/11 membranous, 11/12 membranous or absent, 12/13/14 membranous. Paired dorsal oesophageal pouches in *x*. Intestine begins in *xvi*. Lateral hearts in *x–xii*.

Holandric, testes sacs paired in *x*, single in *xi*, extending to the dorsal line, seminal vesicles in *xi* and *xii*, those of *xi* enclosed in the testes sacs. Pseudoseminal vesicles in *xiii* and occasionally *xiv*. Spermathecae (Fig. 32f) paired in *v–ix*.

DISTRIBUTION. New Guinea.

REMARKS. The types of *ardita*, *myriochaeta* and *tamiensis* differ from the type series of *sentanensis* principally in segment size and setal numbers. The species *tamiensis* was originally described as having four pairs of spermathecae but a re-examination of the single extant syntype revealed the presence of five pairs. In view of the correlation between setal and segmental development these differences do not appear to be taxonomically significant.

Most specimens examined had only presetal genital markings associated with the spermathecal pores, both pre- and postsetal markings were present in a minority which additionally appeared to have slightly lower setal numbers, but no conclusive correlations could be established.

MATERIAL EXAMINED. *Previously reported.* 13C, 3A Near lake Sentani, Jaga (Jocchana), West Irian; Amsterdam Vol. 301 (syntypes of *sentanensis*). 3 other specimens from this series are at Turin (01. 193), they were not examined. 1C Near Tawarin river, west of Mt Cyclops, West Irian; Amsterdam Vol. 289 (holotype of *myriochaeta*). 1C Bivouac 'Zoutbron' on river Begowre, West Irian, 3° 1′ 13″ S, 140° 57′ 30″ E; Leiden 1827 (holotype of *ardita*). 2C, 3A Tami, Papua New Guinea; Berlin 6464 (*ardita*: Ude, 1932). 1C Tami, Papua New Guinea; Berlin 6462 (syntype of *tamiensis*).
New records. 1C, 12A Kaironk valley, Simbai region, Madang district, Papua New Guinea, 1750–1950 m, *coll* R N H Bulmer 8–12 Nov 1973; BMNH 1976.2.8–20. 6A Dense clay with dense organic matter and thin grass cover, side of road adjacent to coffee plantation, Amahab village *c.* 16 km west of Maprik, Sepik district, Papua New Guinea, *coll* J W Copland 12 Nov 1971; BMNH 1976.3.100–105. 2A Dry to moist loam covered by grass and small trees, bank of river, Sepik Plains Livestock Station, Urimo, Sepik district, Papua New Guinea, *coll* J W Copland 1971; BMNH 1976.3.106–107. 10A Moist medium to heavy dark loam with considerable organic content covered by a mat of paspalum, bank of small creek running through No. 12 paddock, Sepik Plains Livestock Station. Urimo, Sepik district, Papua New Guinea, *coll* J W Copland 11 Nov 1971; BMNH 1976.3.108, 109–118. 13C, 8A 15 cm layer of black soil over sandy soil cultivated for gardens, halfway down hill to creek, Department of Agriculture, Stock and Fisheries Piggery, Goroka, Eastern Highlands, Papua New Guinea, *coll* J W Copland 13 Oct 1971; BMNH 1976.3.87–96, 119–129. 1C, 2A Dark sandy loam covered by light vegetation, 120–150 m above Nupa village, *c.* 24 km east of Goroka, Eastern Highlands, Papua New Guinea, *coll* J W Copland 1971; BMNH 1976.1.97, 98–99. 6C, 8A DASF Piggery, Goroka, Papua New Guinea, *coll* J W Copland 13 Oct 1971; BMNH 1977.1.78–81, 141–150. 1C, 1A Bank of creek, DASF Piggery, Goroka, Eastern Highlands, Papua New Guinea, *coll* J W Copland 23 Aug 1972; BMNH 1977.1.100–101. 7C, 1A Locality as above; *coll* J W Copland 1 Sep 1971; BMNH 1977.1.68–75. 1C Nupa village, *c.* 24 km east of Goroka, Eastern Highlands, Papua New Guinea, *coll* J W Copland 13 Oct 1971; BMNH 1977.1.60. 14C, 25A Locality as above, *coll* J W Copland 31 Aug 1971; BMNH 1977.1.102–140. 3C, 1A Moist dense mixture of peat and soil, very rich in humus, Land Resettlement Scheme (area drained 3 years prior to collection), Kendig, Mt Hagen, Western Highlands, Papua New Guinea, *coll* J W Copland 1971; BMNH 1976.3.73–76. 3C, 1A DASF station, Kendig, Mt Hagen, Western Highlands, Papua New Guinea, *coll* J W Copland 15 Nov 1971; BMNH 1977.1.61–63. 3C Moist dark loam of moderate to high organic content, sloping plot being prepared for Kaukau, on boundary of Webag, Mt Hagen, Western Highlands, Papua New Guinea, *coll* J W Copland 16 Nov 1971; BMNH 1976.3.77–78, 79. 9C, 2A Local government council piggery, west of Webag, Mt Hagen, Western Highlands, Papua New Guinea, *coll* J W Copland 16 Nov 1971; BMNH 1976.3.80–86, 1977.1.64–67. 2C Webag, Mt Hagen, Western Highlands, Papua New Guinea, *coll* J W Copland 16 Nov 1971; BMNH 1977.1.76–77. 15C, 3A Kasena, Papua New Guinea, *coll* J W Copland 25 Aug 1972; BMNH 1977.1.82–99. 2C, 1A Madang district, Papua New Guinea, *coll* R. Phipps; BMNH 1976.8.33–35.

Metapheretima lindiae sp. nov.

DIAGNOSIS. *Metapheretima* with simple male pores; numerous spermathecal pores in paired batteries about one fifth of the body circumference apart in furrows 4/5/6/7/8/9. Setal numbers high (cf. *sentanensis*, Fig. 2). Spermathecal diverticula simple, ectal.

DESCRIPTION. *External characters.* Length 54–60 mm, diameter *c.* 1·5 mm. *C.* 105–143 segments. Clitellum *xiv–xvi*. First dorsal pore 11/12. Setae, 94–100 on *vii*, 34–49 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores simple *c.* 0·22 body circumference apart. Female pore(s) not detected. Spermathecal pores small, numerous, arranged in paired batteries of 1–4 in 4/5/6/7/8/9, batteries *c.* 0·23 body circumference apart.

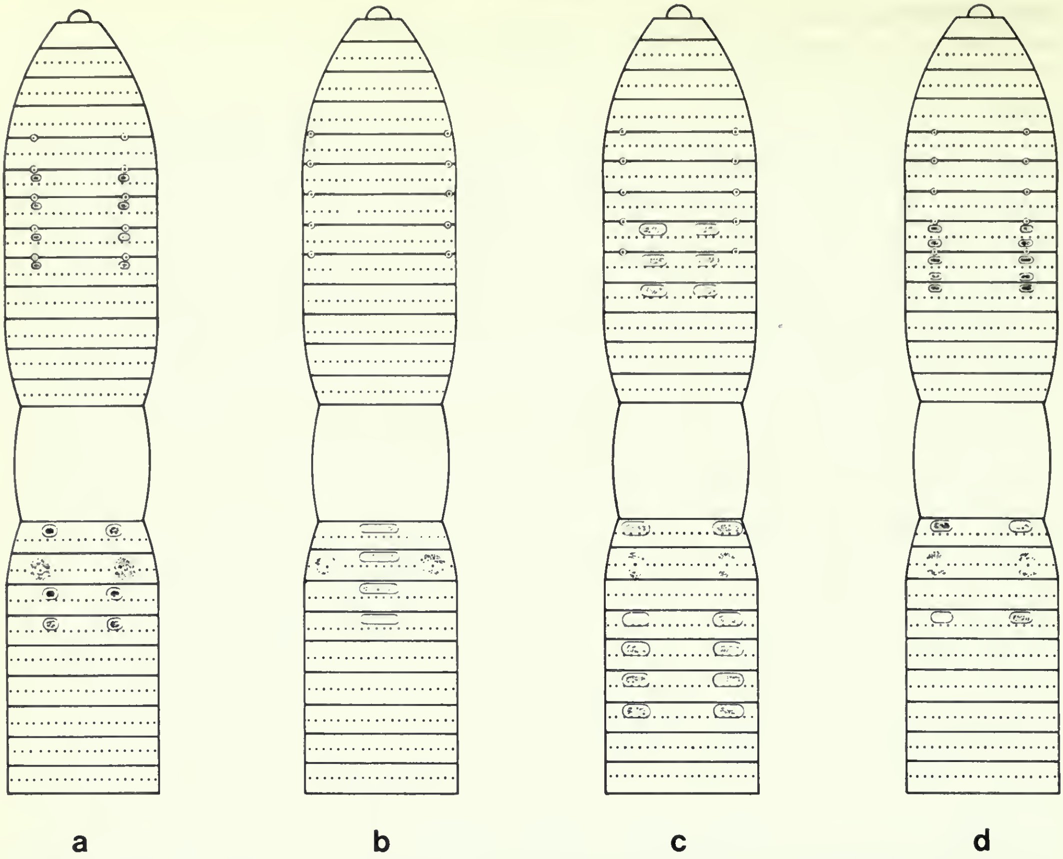

Fig. 35 Anterior ventral surface, diagnostic characters. (a) *Metapheretima quinqueremis* sp. nov.; (b) *M. simsi* sp. nov.; (c) *M. sentanensis*, syntypic individual; (d) *M. sentanensis*, varient individual.

Genital markings (Fig. 34c) paired, presetal on *ix* median to the line of the spermathecal pores, on *xvii*, *xx–xxiii* in line with the male pores.

Internal characters. Septa 5/6/7/8 thickened, 8/9 membranous, 9/10 not detected, 10/11–13/14 slightly thickened. Oesophagus simple. Intestine begins in *xv*. Lateral hearts in *x-xii*.

Metandric, testes sacs large, paired, extending to the dorsal line in *xi*, seminal vesicles large, extending to the dorsal line in *xii*, Pseudoseminal vesicles small in *xiii* and *xiv*. Spermathecae (Fig. 32c) numerous in paired batteries of 1–4 spermathecae in *v–ix*.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 2C Madang district, Papua New Guinea 5° 14′ S, 145° 45′ E, *coll* R Phipps; BMNH 1976.8.1–2 (syntypes of *lindiae*).

Metapheretima queribunda (Gates, 1958)

Pheretima queribunda Gates, 1958 : 25.
Metapheretima queribunda: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one third of the body circumference apart in furrows 4/5/6/7/8/9. Proandric.

DESCRIPTION. *External characters*. Length 75–80 mm, diameter 4–6 mm. 120–135 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, 96–120 on *vii*, *c*. 86 on *xx*, setal ring regular with ventral gaps on postclitellar segments ($aa = 2ab = 2yz = 2zz$).

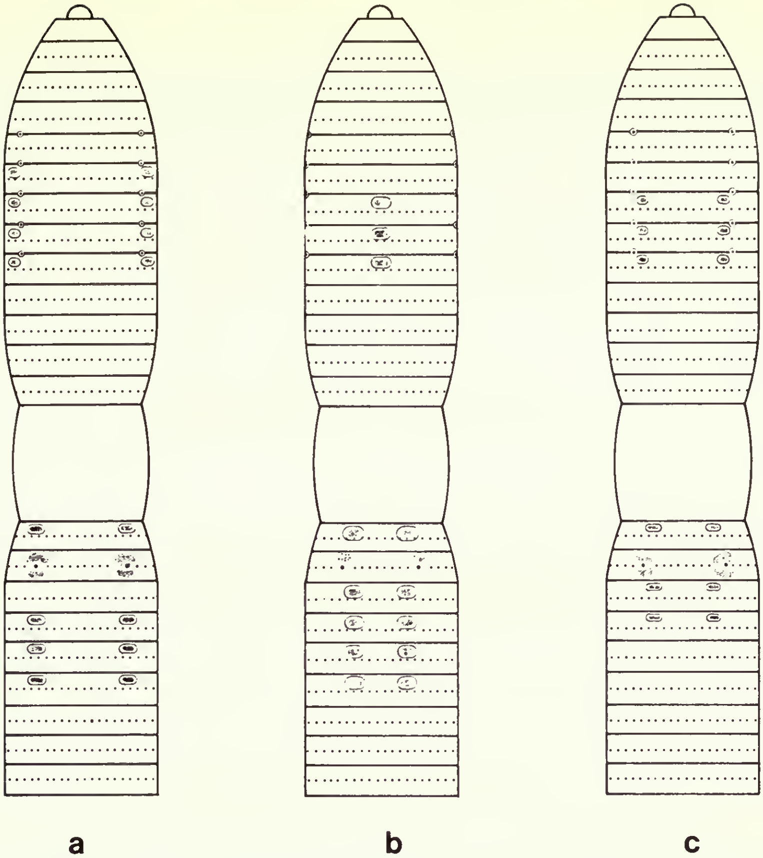

Fig. 36 Anterior ventral surface, diagnostic characters. (a) *Metapheretima queribunda*; (b) *M. pickfordi*; (c) *M. speiseri.*

Male pores simple, *c.* 0·24 body circumference apart. Female pores paired. Spermathecal pores small, paired in 4/5/6/7/8/9, *c.* 0·35 body circumference apart.

Genital markings (Fig. 36a) paired, presetal, slightly lateral to the spermathecal pores on *vi–ix*, in line with the male pores on *xvii*, *xix–xxii.*

Internal characters. Septa 5/6/7/8 thickened, 8/9 membranous or absent, 9/10 absent, 10/11/12/13 membranous. Intestine begins in *xv*. Lateral hearts in *x–xii.*

Proandric, testes sacs paired, extending to the lateral line in *x*, single, extending to the dorsal line in *xi* (but lacking testes), seminal vesicles small, in *xi* enclosed in the testes sacs and *xii*. Pseudoseminal vesicles absent. Spermathecae (Fig. 32g) paired in *v–ix*.

DISTRIBUTION. Solomon Islands.

REMARKS. *M. queribunda* is noteworthy in that, although the posterior pair of testes are absent, the testes sacs of *xi* and the seminal vesicles of *xii* remain. Because of this condition it may be confused with the holandric species of the *bulmeri* species-group.

MATERIAL EXAMINED. *Previously reported.* 1C Gaudalcanal, Solomon Islands; New York 3505 (holotype of *queribunda*).

New record. 1C Under log, Russell Island, Solomon Islands, 15 m; *coll* R A Lever Feb 1934; BMNH 1935.1.18.1.

Metapheretima pickfordi (Gates, 1957)

Pheretima pickfordi Gates, 1957 : 18; Lee, 1969 : 4.

Metapheretima pickfordi: Sims & Easton, 1972 : 231.
? *Perichaeta loriae*: Beddard, 1899 : 185 (*non* Rosa, 1898*b* : 61).

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about half of the body circumference apart in furrows 4/5/6/7/8/9. Setal numbers high (cf. *sentanensis*, fig. 2). Spermathecal diverticula simple, ectal.

DESCRIPTION. *External characters.* Length *c.* 26–28 mm, diameter *c.* 3 mm. *C.* 111 segments. Clitellum *xiv*–$\frac{1}{2}$*xvi*. Dorsal pores not recognized in preclitellar furrows. Setae, 80–90 on *vi*, *c.* 40 on *xx*, setal ring with small dorsal and ventral gaps.

Male pores simple, 'well lateral to the midventral line'. Female pores paired. Spermathecal pores paired in 4/5/6/7/8/9, *c.* 0·50 body circumference apart.

Genital markings (Fig. 36b) presetal, single, median on *vii–ix*, paired, extending laterally as far as the male pores on *xvii*, *xix–xxiii*.

Internal characters. Anterior septa delicate, 8/9 present, 9/10/11 not recognized. Intestine begins in *xv*. Last lateral hearts in *xii*.

Probably metandric, testes sacs single in *xi*, seminal vesicles small in *xii*. Spermathecae, paired in *v–ix*, ampulla elongate, duct short, diverticula slightly longer than main chamber.

Description after Gates (1957); Fig. 36b is an interpretation of the genital field based on Gates's written description.

DISTRIBUTION. Solomon Islands.

REMARKS. It is uncertain whether *M. pickfordi* is holandric or metandric. Gates (1957) could not recognize the testes in *x* because of the decomposed condition of the type series and Lee (1969) did not comment on the condition of the testes in the specimens he examined.

RECORDS. 1C, 1A Coconut grove, Lavanggu, Rennell Island, Solomon Islands (types of *pickfordi*). Guadalcanal (*pickfordi*: Lee, 1969).

Metapheretima speiseri (Michaelsen, 1913)

Pheretima speiseri Michaelsen, 1913*b* : 263.
Pheretima (*Pheretima*) *speiseri*: Pickford, 1929 : 493.
Planapheretima speiseri: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores; spermathecal pores about one third of the body circumference apart in furrows (4/5/6) 6/7/8/9. Holandric. Setal numbers intermediate (cf. *elongata*, fig. 2). Spermathecal diverticula simple, ectal.

DESCRIPTION. *External characters.* Length 26–80 mm, diameter 2–3 mm. 78–96 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, 32–54 on *vii*, 36–56 on *xx*, setal ring regular, occasionally with slight ventral gaps ($aa = 1\text{–}1{\cdot}5ab = yz = zz$).

Male pores simple, *c.* 0·22 body circumference apart. Female pores paired. Spermathecal pores small, paired in 6/7/8/9 and usually 5/6 and 4/5, *c.* 0·26–0·40 body circumference apart.

Genital markings (Fig. 36c), paired, presetal, median or slightly lateral to the line of the spermathecal pores on *vii–ix*, in line with the male pores on *xvii*, *xix–xx*.

Internal characters. Septa 5/6/7/8 slightly thickened, 8/9 membranous or absent, 9/10–13/14 slightly thickened. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Holandric, testes sacs paired, small, ventral in *x* and *xi*, seminal vesicles extending to the dorsal line in *xi* and *xii*. Spermathecae (Fig. 32h) paired, usually in *v–ix*, those of *v* and *vi* may be absent.

DISTRIBUTION. New Hebrides.

REMARKS. The type series of *speiseri* and the specimens identified by Pickford (1929) display considerable variation in the development of the posterior male organs and spermathecae. Michaelsen (1913) recognized two conditions (A and B) and Pickford (1929) a third (C) to which she provided the following diagnosis:

A-form without prostates and male pores but with fully developed spermathecae.
B-form with prostates and male pores but with reduced spermathecae.
C-form with prostates, male pores and fully developed spermathecae.
Variation of this kind is often encountered among the species of the *Pheretima* group, especially in introduced populations where it has been utilized to establish the indigenous range of some species (Gates, 1956; Easton, 1976). It is not considered to have any taxonomic significance. Nevertheless, the single example examined of form A has more widely paired spermathecal pores (*c.* 0·40) than individuals of both forms B and C (*c.* 0·26), and more closely paired preclitellar genital markings.

MATERIAL EXAMINED. *Previously reported.* 2C Espiritu Santo, New Hebrides; Hamburg v8071 (syntypes of *speiseri*). 8A Summit of Tabwe Masana, Espiritu Santo, New Hebrides; BMNH 1929.6.11.1–7 (*speiseri*: Pickford, 1929). 1C, 2A Near shore of lake, Gaua, New Hebrides; BMNH 1928.3.22.11 (*speiseri*: Pickford, 1929). Fragments of 1C, data as above; Hamburg v11966 (*speiseri*: Pickford, 1929).
New record. 6C Tatarii, west Santo, New Hebrides; BMNH 1934.3.6.24–26.

Metapheretima elrondi sp. nov.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one quarter of the body circumference apart in furrows 5/6/7/8/9. Holandric. Setae numerous (cf. *sentanensis*, Fig. 2). Spermathecal diverticula simple.

DESCRIPTION. *External characters.* Length 50–133 mm, diameter *c.* 5 mm. *C.* 106 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, 88–220 on *vii*, 40–60 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores simple, *c.* 0·25 body circumference apart. Female pores paired. Spermathecal pores small, paired in 5/6/7/8/9, *c.* 0·25 body circumference apart.

Genital markings (Fig. 37a) paired, presetal, slightly median to the line of the spermathecal pores on *ix–xi*, slightly median to the line of the male pores on *xvii*, *xx–xxiii*.
Internal characters. Septa 5/6/7/8 thickened, 8/9 slightly thickened, 9/10 and succeeding septa delicate. Intestine begins in *xvi*. Lateral hearts in *x–xii*.

Holandric, testes sacs paired, ventral with dorsal connections over the oesophagus in *x* and *xi*; seminal vesicles small, those of *xi* enclosed in the testes sacs. Pseudoseminal vesicles in *xiv*. Spermathecae (Fig. 32i) paired in *vi–ix*.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 6C, 3A Soil of alluvial clay derived from gabbro, pH 5·5–6·3, highly humidified, organic content 15–30%, C/N ratio 8–9. Gentle ridge covered in mixed lower montane forest with *Podocarpus*, Eleocarpace, Lauracae, Cunoniaceae dominant, Bismark range, Eastern Highland district, Papua New Guinea, 5° 58′ S, 145° 15′ E, rainfall 890 cm/year, altitude 2500 m, *coll* D R Kershaw 20 Jul 1971; BMNH 1976.5.116–124 (syntypes of *elrondi*). 13C, 18A Locality and collector as above; BMNH 1976.5.125–156. 2C, 4A Locality and collector as above; Papua New Guinea.

Metapheretima sola sp. nov.

DIAGNOSIS. *Metapheretima* with simple male pores; closely paired spermathecal pores in furrows 5/6/7/8/9. Metandric. Setae sparse (cf. *kinabaluensis*, Fig. 2). Spermathecal diverticula simple, ectal.

DESCRIPTION. *External characters.* Length *c.* 96 mm, diameter *c.* 4 mm. *C.* 76 segments. Clitellum *xiv–xvi*, first dorsal pore 12/13. Setae, *c.* 27 on *vii*, *c.* 41 on *xx*, setal ring slightly crowded ventrally ($2aa = 2ab = yz = zz$).

Male pores simple, *c.* 0·08 body circumference apart. Female pores paired. Spermathecal pores large, paired, in 5/6/7/8/9, *c.* 0·08 body circumference apart.

Genital markings (Fig. 37b), paired, presetal, in line with the spermathecal pores on *vi–ix*, in line with the male pores on *xvii*, *xix–xxi*.

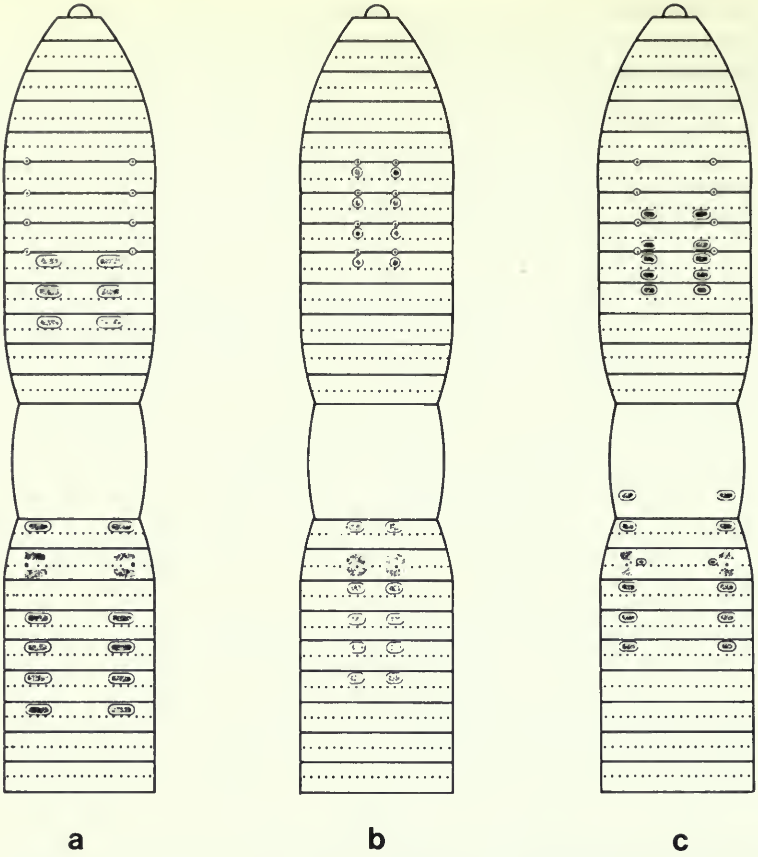

Fig. 37 Anterior ventral surface, diagnostic characters. (a) *Metapheretima elrondi* sp. nov.; (b) *M. sola* sp. nov.; (c) *M. triciae* sp. nov. typical individual.

Internal characters. Septa 5/6/7/8 membranous, 8/9 absent, 9/10–12/13 slightly thickened. Oesophagus with slight, dorsolateral pouches in *xi*. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs large, paired, ventral in *xi*, seminal vesicles large, extending to the dorsal line in *xii*. Pseudoseminal vesicles absent. Spermathecae (Fig. 32j) paired in *vi–ix*.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 1C Mt Suckling, Papua New Guinea, 9° 46′ S, 149° 00′ E, *coll* W H Ewer Jun 1972; BMNH 1976.4.63 (holotype of *sola*).

Metapheretima triciae sp. nov.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores one third to one sixth of the body circumference apart in furrows 5/6/7/8/9. Metandric. Setal numbers high (Fig. 2). Spermathecal diverticula simple, ectal.

DESCRIPTION. *External characters.* Length 65–114 mm, exceptionally 235 mm, diameter 3–5 mm, exceptionally 8 mm. 110–156 segments. Clitellum *xiv–xvi*. First dorsal pore 11/12 or 12/13. Setae, 100–135 (188) on *vii*, 41–60 (140) on *xx*, setal ring usually single, occasionally double on *iv–xi*; regular with dorsal and ventral gaps on postclitellar segments ($aa = 2ab = 2yz = zz$).

Male pores simple, 0·17–0·26 body circumference apart. Female pores single or paired. Spermathecal pores small, paired, in 5/6/7/8/9, 0·14–0·35 body circumference apart.

Genital markings highly variable (Figs 37c, 38) paired, presetal on *vi–x*, postsetal on *vi–ix*, one or more pairs, presetal on *xvi–xxiii*, postsetal on *xvii*.

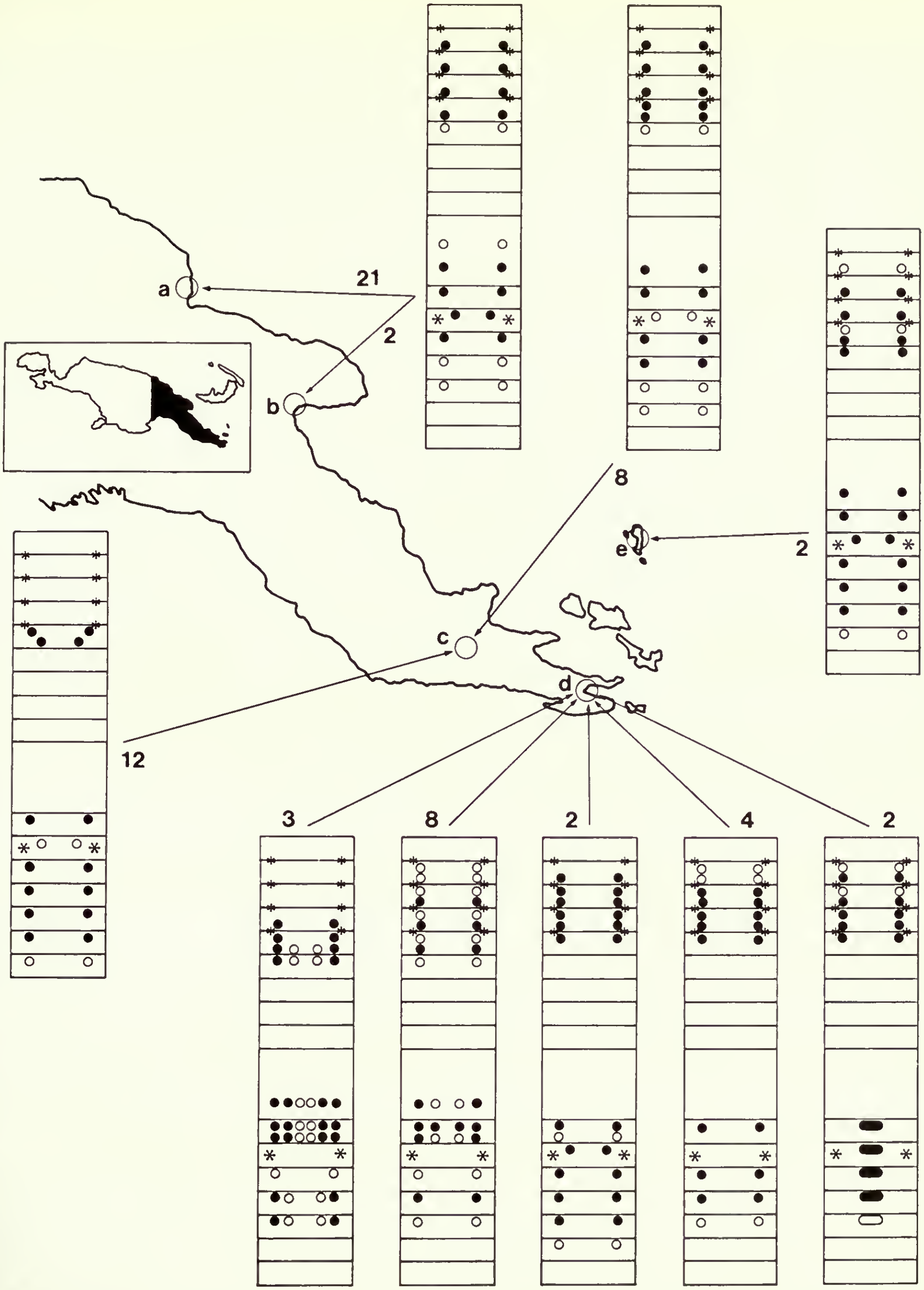

Fig. 38 *Metapheretima triciae* sp. nov. Ventral markings: geographical variations. (a) Madang (type locality); (b) Langemak Bay; (c) Mt Suckling; (d) Milne Bay; (e) Trobriand Islands. Numerals indicate numbers of clitellate individuals examined. Closed circles – markings invariably present; open circles – markings occasionally present.

Internal characters. Septa 5/6/7/8 thickened. 8/9/10 membranous or absent, 10/11–12/13 membranous. Oesophagus simple or with small, dorsolateral pouches in *x*. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs large paired, often joined above the intestine, in *xi*, seminal vesicles reaching the dorsolateral or dorsal line in *xii*. Pseudoseminal vesicles in *xiii*. Spermathecae (Fig. 32k) paired in *v–ix*.

DISTRIBUTION. East and northeast New Guinea.

REMARKS. The genital markings of this species are variable although usually constant in specimens from one locality. It has not been possible to establish any correlations between the many papillae patterns, the various distances separating the spermathecal pores and the conditions of the testes sacs; for convenience, therefore, populations possessing these variations are not separated taxonomically.

MATERIAL EXAMINED. 22C, 1A Waterlogged dark sandy loam with a high organic content, vegetation of ferns, grass and coconut, close to sea, Bunu village no 2, Madang district, Papua New Guinea, 4° 52′ S, 145° 49′ E, *coll* J W Copland 14 Nov 1971; BMNH 1976.3.130–154 (syntypes of *triciae*). 12C, 8A Data as above; BMNH 1977.1.153–172. 15C, 18A Mau 1, Mt Suckling, Papua New Guinea, *coll* W H Ewers Jun 1972; BMNH 1976.4.7–29, 68–81, 140. 15C, 8A Samarai, Milne Bay, Papua New Guinea, *coll* J W Copland 21 Jul 1971; BMNH 1977.1.173–194. 4A Sineada, Milne Bay, Papua New Guinea, *coll* J W Copland 22 Jul 1971; BMNH 1977.1.197–200. 2C, Trobriand Islands, Papua New Guinea, *coll* J W Copland; BMNH 1977.1.195–196. 3C, 1A Papua New Guinea (label completely destroyed), *coll* J W Copland; BMNH 1977.1.201–204. 2C, 1 posterior fragment, rotting stems of wood at waterfall Langemak Bay, east Coast, Papua New Guinea; Hamburg 01.13177 (specimens separated from type series of *M. pallens* (Ude, 1932)).

Metapheretima trukensis (Ohfuchi, 1940)

Pheretima trukensis Ohfuchi, 1940 : 24.
Metapheretima trukensis: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores; closely paired spermathecal pores in furrows 5/6/7/8.

DESCRIPTION. *External characters.* Length 189–193 mm, diameter 6·7–7·3 mm. 130–135 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae 36–38 on *vii*, 75–80 on *xx*, details of setal ring not recorded.

Male pores 'minute' on conical papillae or circular porophores (Ohfuchi, 1940 was unable to detect which of the structures on *xviii* carried the male pores), separation not recorded. Female pores not recorded. Spermathecal pores paired in 5/6/7/8, *c.* 0·10 body circumference apart.

Genital markings (Fig. 39a) several paired markings, presetal on *xix–xxi*, postsetal on *xvii*, *xviii*.

Internal characters. Septa 5/6/7 thickened, 8/9/10 absent, 10/11–14/15 thickened. Intestinal origin *xx*. Lateral hearts not recorded. Holandric; testes sacs annular, *x*, *xi* seminal vesicles small, *xi*, *xii*. Spermathecae (Fig. 32l) paired in *vi–viii*. Description after Ohfuchi (1940).

DISTRIBUTION. Truk, east Carolines.

REMARKS. This species has been assigned to the genus *Metapheretima* on the affinities revealed during the numerical studies (see above), since it is uncertain whether the intersegmental genital markings associated with the male pores are crescentic genital markings. *M. trukensis* possesses several morphological features atypical of the genus. There are two pairs of presetal genital markings and the intestine begins in *xx*.

RECORDS. 3 or more specimens Natsushima of Truk, east Carolines Islands (syntypes of *trukensis*).

Metapheretima carolinensis (Michaelsen, 1910)

Pheretima carolinensis Michaelsen, 1910*b* : 105; Ohfuchi, 1940 : 7.
Pheretima (*Polypheretima*) *carolinensis*: Michaelsen, 1934*b* : 15.

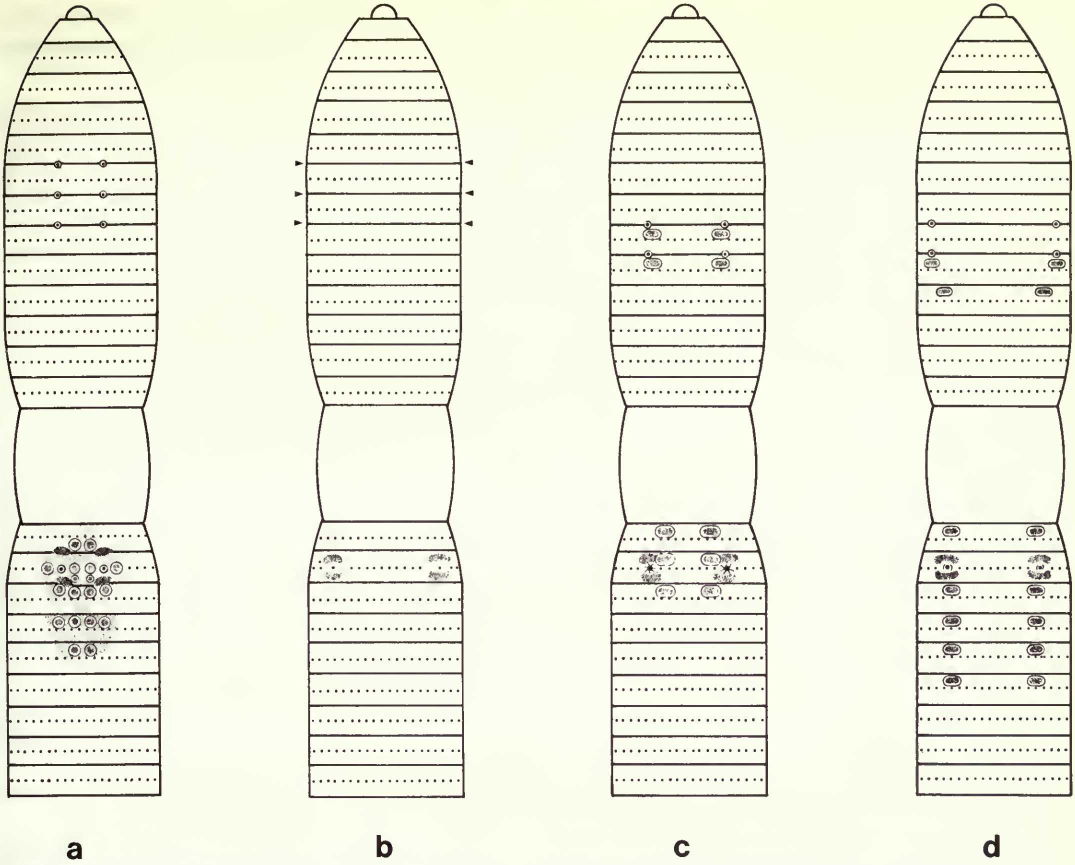

Fig. 39 Anterior ventral surface, diagnostic characters. (a) *Metapheretima trukensis*; (b) *M. carolinensis*, arrows indicate furrows with numerous dorsal spermathecal pores; (c) *M. sembaluensis*; (d) *M. pallens*.

Metapheretima carolinensis: Sims & Easton, 1972 : 233.
Pheretima garama Gates, 1958 : 8.
Metapheretima garama: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores; numerous, dorsally placed spermathecal pores in furrows 5/6/7/8.

DESCRIPTION. *External characters.* Length 47–191 mm, diameter 3–7 mm. 86–134 segments. Clitellum *xiv–xvi*. First dorsal 11/12 or 12/13. Setae, 33–53 on *vii*, 57–70 on *xx*, setal ring regular with dorsal gaps on postclitellar segments (*aa*=*ab*=*yz*=0·5*zz*).

Male pores simple, *c.* 0·26 body circumference apart. Female pore single. Spermathecal pores small transverse slits, numerous in paired batteries in 5/6/7/8, *c.* 0·90 body circumference apart.

Genital markings, absent apart from those diagnostic of the genus (Fig. 39b).

Internal characters. Septa 5/6/7/8 thickened, 8/9/10 absent, 10/11–14/15 thickened. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Holandric, testes sacs paired, extending to the lateral line in *x* and to the dorsal line in *xi*, seminal vesicles of *xi* extending to the lateral line and enclosed in the testes sacs, those of *xii* extending to the dorsal line. Pseudoseminal vesicles in *xiv*. Spermathecae (Fig. 32m) paired batteries of up to 8 spermathecae in *vi–viii*.

DISTRIBUTION. Caroline Islands.

REMARKS. The original description of *M. garama* differs from the type series of *carolinensis* only by its smaller size and lower setal numbers. These differences do not appear to be taxonomically significant.

MATERIAL EXAMINED. 2C Caroline Islands; Hamburg v3310 (syntypes of *carolinensis*). 1C Tokongo Islet, Kapingamarangi, south Caroline Islands; New York 3569 (holotype of *garama*). The original description of *garama* was based on a further 6C and 9A paratypes; their present location is unknown.

OTHER RECORDS. 8 specimens Angaul Island, Caroline Islands (*carolinensis*: Ohfuchi, 1940).

Metapheretima sembaluensis (Ude, 1932)

Pheretima (*Pheretima*) *sembaluensis* Ude, 1932 : 139.
Metapheretima sembaluensis: Sims & Easton, 1972 : 233.
Pheretima (*Pheretima*) *rosai* Ude, 1932 : 140.
Metapheretima rosai: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one fifth of the body circumference apart in furrows 7/8/9. Holandric. Spermathecal diverticula simple, ectal.

DESCRIPTION. *External characters*. Length 100–210 mm, diameter 4–8 mm. 140–150 segments. Clitellum *xiv–xvi*. First dorsal pore 11/12 or 12/13. Setae, 60–120 on *vii*, 70–80 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores, large, simple, *c*. 0·20 body circumference apart. Female pore single. Spermathecal pores large, paired in 7/8/9, *c*. 0·20 body circumference apart.

Genital markings (Fig. 39c) paired, presetal, slightly median to the line of the spermathecal pores, on *viii* and *ix*, slightly median to the male pores, on *xvii–xx*, the pair of markings on *xviii* may be fused to form a single median marking.

Internal characters. Anterior septa present and thickened. Intestine begins in *xv*. Lateral hearts in *x–xii* and occasionally *xiii*.

Holandric, testes sacs small, paired, ventral in *x* and *xi*, seminal vesicles extending to the dorsal line in *xi* and *xii*. Pseudoseminal vesicles large in *xiii*. Spermathecae (Fig. 32n) paired in *viii–ix*.

DISTRIBUTION. Lombok.

REMARKS. Ude (1932) described *sembaluensis* and *rosai* on material from Lombok with single (median) and paired genital markings respectively in the region of the male pores. More recently collected series exhibit a tendency for the paired genital markings to meet and coalesce to form a single median marking, on this evidence it is proposed to synonomize the two taxa.

M. sembaluensis is the only known species of *Metapheretima* occurring in Lombok where it represents the most westerly record of the genus.

MATERIAL EXAMINED. *New records*. 4A, 1A Surawadi, Lombok, 400 m, *coll* G Lincoln 10 Aug 1973; BMNH 1975.7.15–18. 7C, 1A Bentak halfway between Tandjung and Mataram, Lombok 400 m, *coll* G Lincoln 12–13 Aug 1973; BMNH 1975.7.19–27.

OTHER RECORDS. Plateau enclosed by crater wall, Rinjani district, Sembalun, Lombok, 1200 m (type(s) of *sembaluensis*). Lake Tihoe, Ladjang, Lombok (type(s) of *rosai*).

Metapheretima pallens (Ude, 1932 : 170)

Pheretima (*Metapheretima*) *pallens* Ude, 1932 : 170.
Metapheretima pallens: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one third of the body circumference. Metandric. Spermathecal diverticula simple.

DESCRIPTION. *External characters*. Length 38–130 mm, diameter 4–5 mm. 90–102 segments. Clitellum *xiv–xvi*. First dorsal pore 11/12. Setae, 146–156 on *vii*, 25–30 on *xx*, setal ring regular on preclitellar segments (*aa*=*ab*=*yz*=*zz*), slightly crowded ventrally with ventral gaps on postclitellar segments (*aa*=2*ab*=*yz*=*zz*).

Male pores small transverse slits, *c.* 0·21 body circumference apart. Female pores single. Spermathecal pores large, paired in 7/8/9, *c.* 0·31 body circumference apart.

Genital markings (Fig. 39d) paired, presetal, directly posterior to the spermathecal pores on *viii* and *ix*, more medianly placed on *x* and *xi*, in line with the male pores on *xvii*, *xx–xxv*.

Internal characters. Septa 5/6/7/8 thickened, 8/9 absent, 9/10 membranous, 10/11 absent, 11/12/13/14 membranous. Oesophagus with paired dorsal pouches in *x–xi*. Intestine begins in *xvi*. Lateral hearts in *xi–xiii.*

Metandric, testes sacs small, paired, reaching the lateral line in *xi*, seminal vesicles extending to the dorsal line in *xii*. Pseudoseminal vesicles small in *xiv*. Spermathecae (Fig. 32o) paired in *viii–ix*.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. *Previously reported.* 2C, 11A From rotting stems in woodland near waterfall, Langemak bay, east coast, Papua New Guinea; Hamburg v3482 (syntypes of *pallens*). This series was contained in a jar with a museum label on which was written a manuscript name '. . . n. sp. Ude, 1926'. On examination the specimens were found to form two series. The first one agrees closely with the description of *M. pallens*, and since the collecting details also agree with those provided by Ude (1932) the material can be regarded as the hitherto missing type series of the species. The specimens forming the second series are described above under the name *M. triciae*.

New records. 10C Very wet black soil, Woitape Station, Goilala, Papua New Guinea, 1600 m, *coll* J W Copland; BMNH 1977.1.50–59. 2C Side of creek, Faripe road, Woitape, Goilala, Papua New Guinea, 1850 m, *coll* J W Copland; BMNH 1977.1.47–49. 2C, 2A Guarimeipa, Papua New Guinea, 1500 m, *coll* J W Copland 7 Dec 1973; BMNN 1977.1.43–46. 11C, 6A Umboli, Papua New Guinea, 1800–2400 m, *coll* Griffiths 1972; BMNH 1976.10.1.18.

Metapheretima neoguinensis species-group

DIAGNOSIS. *Metapheretima* with simple male pores lacking associated glandular ridges. Spermathecal diverticula multilocular, ectal.

SPECIES INCLUDED. *deirdrae*, *loriae*, *neoguinensis*, *septocta*, *sucklingensis*.

DISTRIBUTION. South-east New Guinea, New Britain, ? Solomon Islands.

REMARKS. The species forming the *neoguinensis* species-group are readily distinguished from one another by the distribution of their spermathecal pores; *loriae*, 4/5/6/7/8/9; *neoguinensis*, 5/6/7/8/9; *sucklingensis*, 6/7/8/9; *deirdrae*, 7/8/9 and *septocta*, 7/8. All of the members of this species-group are metandric but in view of the low information value of metandry in other species-groups of *Metapheretima*, this character is not regarded as being diagnostic of the group.

Metapheretima loriae (Rosa, 1898)

Perichaeta loriae Rosa, 1898*b* : 61; ? Beddard, 1899 : 185 (? =*M. pickfordi*).
Amynthas loriae: Beddard, 1900*a* : 641.
Pheretima loriae: Michaelsen, 1900 : 281; Ude, 1905 : 481.
Metapheretima loriae: Sims & Easton, 1972 : 231.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one quarter of the body circumference apart in furrows 4/5/6/7/8/9. Metandric. Spermathecal diverticula multilocular, ectal.

DESCRIPTION. *External characters.* Length 120–130 mm, diameter *c.* 6 mm. *C.* 99 segments. Clitellum *xiv–xvi*. First dorsal pore 11/12 or 12/13. Setae, 51–63 on *vii*, 52–60 on *xx*, setal ring regular on preclitellar segments (*aa*=*ab*=*yz*=*zz*), slightly crowded ventrally on postclitellar segments (*aa*=*ab*=0·5*yz*=0·5*zz*).

Male pores simple, 0·14–0·20 body circumference apart. Female pores paired. Spermathecal pores small, paired in 4/5/6/7/8/9, 0·20–0·28 body circumference apart.

Genital markings (Fig. 40a) paired, presetal, slightly median to the line of the spermathecal pores, on *viii* and *ix*, slightly median to the male pores on *xvii*, *xix* and *xx*.

Internal characters. Septa 5/6–11/12 membranous, 12/13/14 thickened. Intestine begins in *xv*. Lateral hearts in *x-xiii.*

Metandric, testes sacs small, paired in *xi*, seminal vesicles large, reaching to the dorsal line in *xii*. Spermathecae (Fig. 33a) paired in *v–ix*, diverticula multilocular.

DISTRIBUTION. New Guinea, ? Solomon Islands.

REMARKS. The record of *loriae* from the Solomon Islands (Beddard, 1899) is dubious since there is no reference to the presence of the diagnostic multilocular spermathecal diverticula; unfortunately this material cannot be located. It is more likely that Beddard's material was of the species *M. pickfordi* which is known only from the Solomon Islands, has only simple spermathecal diverticula and is probably metandric.

MATERIAL EXAMINED. *Previously reported.* 2C, 1A 'Hughibagu', Papua New Guinea; Genova 37 (syntypes of *loriae*). This locality cannot be traced, possibly the name is a corruption of Hughes Bay, Furgusson Islands, 9° 23′ S, 150° 42′ E, which is near other places visited by the same collector.

New record. 1C Mt Suckling, Papua New Guinea, *coll* W H Ewers 15 Jun 1972; BMNH 1976.4.3.

OTHER RECORDS. 2 specimens, Guadalcanal, Solomon Islands (*loriae*: Beddard, 1899).

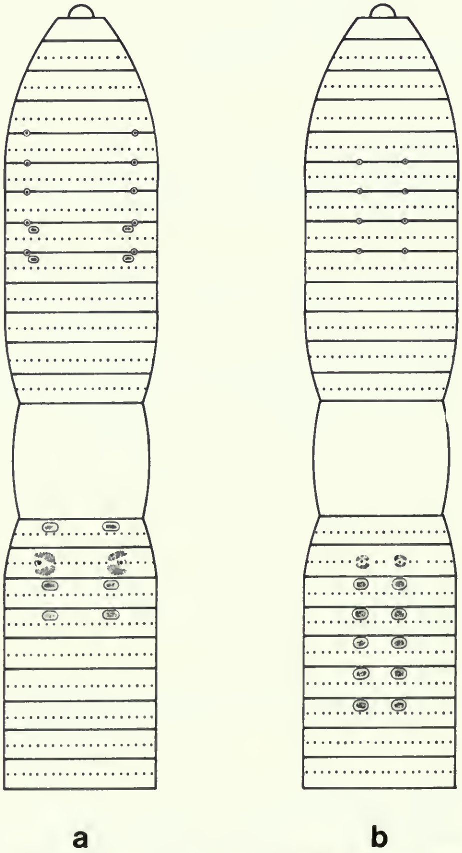

Fig. 40 Anterior ventral surface, diagnostic characters. (a) *Metapheretima loriae*; (b) *M. neoguinensis*.

Metapheretima neoguinensis (Michaelsen, 1892)

Perichaeta neoguinensis Michaelsen, 1892 : 299.
Amynthas neoguinensis (part, i.e. acaecate specimens): Beddard, 1900*a* : 642.
Pheretima neoguinensis: Michaelsen, 1900 : 288; Ude, 1905 : 481; (syn. *helvola*) Ude, 1932 : 173.
Pheretima (*Metapheretima*) *neoguinensis*: Michaelsen, 1928*a* : 7.
Metapheretima neoguinensis: Sims & Easton, 1972 : 205, 233.
Pheretima helvola Ude, 1905 : 473 [non Michaelsen, 1934*c* : 520 (=*Metaphire hobaensis* Gates, 1941)].
Metapheretima helvola: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores less than one tenth of the body circumference apart in furrows 5/6/7/8/9. Metandric. Spermathecal diverticula multilocular, ectal.

DESCRIPTION. *External characters.* Length 140–150 mm, diameter 6–9 mm. 94–124 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13 or 13/14. Setae, 78–98 on *vii*, 66–86 on *xx*, setal ring regular with dorsal and ventral gaps on postclitellar segments ($aa = 1{\cdot}5ab = 1{\cdot}5yz = zz$).

Male pores simple, 0·06–0·12 body circumference apart. Female pore paired or single. Spermathecal pores small, paired, in 5/6/7/8/9, 0·02–0·08 body circumference apart.

Genital markings (Fig. 40b) paired, presetal in line with the male pores on *xix–xxiii*.
Internal characters. Septa 5/6/7/8 thickened, 8/9 membranous, 9/10 membranous or absent, 10/11–13/14 thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

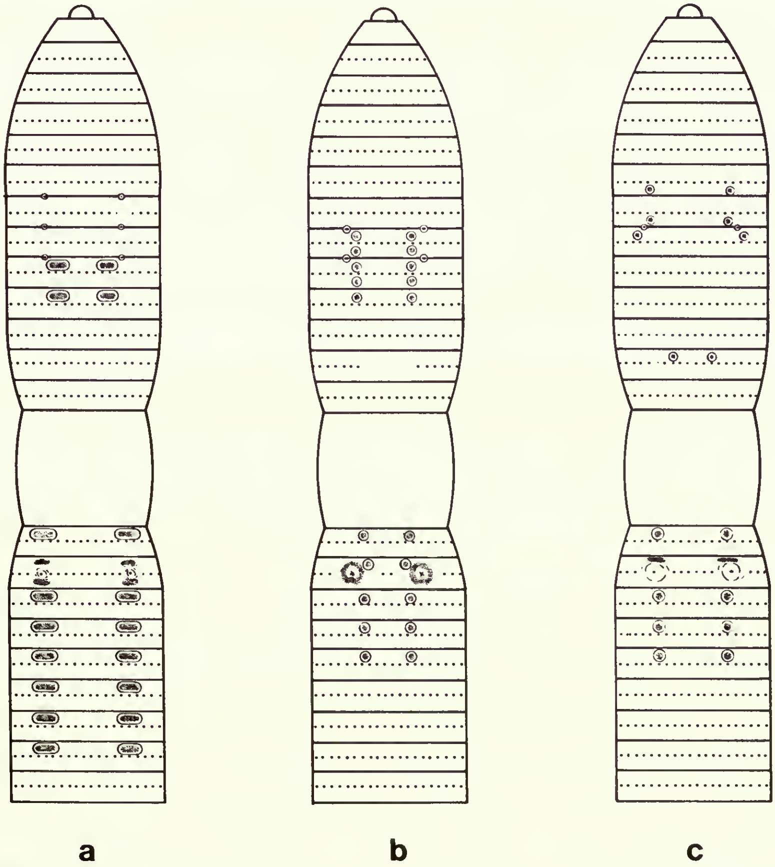

Fig. 41 Anterior ventral surface, diagnostic characters. (a) *Metapheretima sucklingensis* sp. nov.; (b) *M. dierdrae* sp. nov.; (c) *M. septocta*.

Metandric, testes sacs small, paired, ventral in *xi*, seminal vesicles large, extending to the dorsal line in *xii*. Pseudoseminal vesicles vestigial in *xiii* or absent. Spermathecae (Fig. 33b) paired in *vi–ix*, diverticula multilocular.

DISTRIBUTION. New Guinea, New Britain.

REMARKS. Rosa (1898) described *spectablis* as a variety of *neoguinensis* but Beddard (1900*a*) placed them together in synonymy. Michaelsen (1900) restricted the definition of *neoguinensis* and recognized *spectablis* as a distinct species which Sims & Easton (1972) assigned to the genus *Amynthas*.

The type series of *helvola* could not be located during the preparation of this report so it has not been possible to evaluate Ude's decision (1932) to place this species within the synonomy of *neoguinensis*.

MATERIAL EXAMINED. *Previously reported.* 1C New Guinea; Hamburg v332 (syntype of *neoguinensis*). 2C New Guinea; Berlin 2133 (syntypes of *neoguinensis*).
New record. 1C, 2A Port Moresby, Papua New Guinea, *coll* W E Ewer Apr 1967; BMNH 1976.4.4–6.

OTHER RECORDS. Ralum, New Britain (type(s) of *helvola* Ude, 1905).

Metapheretima sucklingensis sp. nov.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one quarter of the body circumference apart in furrows 6/7/8/9. Metandric. Spermathecal diverticula multilocular, ectal.

DESCRIPTION. *External characters.* Length *c.* 175 mm, diameter *c.* 6 mm. *C.* 160 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae 51–76 on *vii*, 53–57 on *xx*, setal ring regular with dorsal and ventral gaps ($aa = 2ab = 2yz = zz$).

Male pores simple on small spherical porophores 0·23–0·28 body circumference apart. Female pores paired. Spermathecal pores small, paired in 6/7/8/9, *c.* 0·16–0·33 body circumference apart.

Genital markings (Fig. 41a), paired, presetal, median to the line of the spermathecal pores on *ix* and *x*, in line with the male pores on *xvii*, *xix–xxiv*.

Internal characters. Septa 5/6/7/8 thickened, 8/9 absent, 9/10–12/13 thickened. Oesophagus slightly pouched in *x*, *xi*. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs small, paired, ventral in *xi*, seminal vesicles extending to the dorsal line in *xii*. Pseudoseminal vesicles vestigial in *xiv*. Spermathecae (Fig. 33c) paired in *vii–ix*, diverticula multilocular.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 2C, 1A Mt Suckling, Papua New Guinea, 9° 46′ S, 149° 00′ E, *coll* W H Ewer 1972; BMNH 1976.4.64–66 (syntypes of *sucklingensis*). 1C In large bunches of fruits of *Fucus* sp., close to ground, Mt Suckling, Papua New Guinea, *coll* G Leach 5 Jul 1972; BMNH 1976.4.67.

Metapheretima deirdrae sp. nov.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one fifth of the body circumference apart in furrows 7/8/9. Metandric. Spermathecal diverticula multilocular, ectal.

DESCRIPTION. *External characters.* Length 180–210 mm, diameter 5–7 mm. 250–259 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, *c.* 110 on *vii*, *c.* 88 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores large, each surrounded by an annulus of pigmented epidermis, *c.* 0·14 body circumference apart. Female pores paired. Spermathecal pores large, paired in 7/8/9, *c.* 0·19 body circumference apart.

Genital markings (Fig. 41b) paired, pre- and postsetal on *vii–x*, slightly median to the line of the spermathecal pores, presetal slightly median to the male pores on *xvii–xxi*.
Internal characters. Septa 5/6–7/8 thickened, 8/9 membranous, 9/10–13/14 membranous. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Metandric, testes sacs small, paired extending to the lateral line in *xi*, seminal vesicles in *xii*. Spermathecae (Fig. 33d) paired in *viii* and *ix*, diverticula multilocular.

DISTRIBUTION. New Guinea.

REMARKS. The crescentic markings diagnostic of the genus *Metapheretima* are apparently absent from the type series of this species although the annuli of pigmented epidermis surrounding the male pores may represent a modified form of these markings. The species has many affinities with other members of the *Metapheretima neoguinensis* species group including the presence of multilocular spermathecal diverticula.

MATERIAL EXAMINED. 2C, 3A Slope in sun with only a little vegetation, Lavavai, Papua New Guinea 8° 23′ S, 147° 03′ E, 1600 m, *coll* J W Copland; BMNH 1977.1.4–8 (syntypes of *deirdrae*).

Metapheretima septocta sp. nov.

DIAGNOSIS. *Metapheretima* with simple male pores; paired spermathecal pores about one fifth of the body circumference apart in furrow 7/8. Metandric. Spermathecal diverticula multilocular, ectal.

DESCRIPTION. *External characters.* Length *c.* 103 mm, diameter *c.* 4 mm. *C.* 112 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, *c.* 43 on *vii*, *c.* 46 on *xx*, setal ring regular with ventral gaps on preclitellar segments ($aa = 2ab = 2yz = 2zz$), with dorsal and ventral gaps on postclitellar segments ($aa = 2ab = 2yz = zz$).

Male pores small transverse slits on spherical porophores, *c.* 0·19 body circumference apart. Female pore single. Spermathecal pores small paired transverse slits in 7/8, *c.* 0·22 body circumference apart.

Genital markings (Fig. 41c), paired, presetal on *viii*, lateral to the spermathecal pores and on *xii* median to the spermathecal pores, postsetal on *vi* and *vii* median to the spermathecal pores, presetal on *xvii*, *xix–xxi* slightly median to the male pores.
Internal characters. Septa 5/6/7/8 thickened, 8/9 absent, 9/10–13/14 slightly thickened, intestine begins in *xvi*. Lateral hearts in *x–xiii*.

Metandric, testes paired, extending to the lateral line in *xi*, seminal vesicles large, extending to the dorsal line in *xii*. Spermathecae (Fig. 33e) paired in *viii*, diverticula multilocular.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 8C Mt Suckling, Papua New Guinea, 9° 46′ S, 149° 00′ E, *coll* W H Ewer Jun 1972; BMNH 1976.4.55–62 (syntypes of *septocta*).

Metapheretima durendali species-group

DIAGNOSIS. *Metapheretima* with male pores on penes within copulatory pouches; large paired spermathecal pores, usually in several furrows. Spermathecal diverticula simple, ectal in origin. Glandular ridges associated with the male pores absent.

SPECIES INCLUDED. *durendali*, *excalaberi*.

DISTRIBUTION. New Guinea.

REMARKS. Although members of this group and the *oinakensis* species-group closely resemble one another, *durendali* and *excalaberi* may be distinguished externally by their more numerous, anteriorly situated spermathecal pores and internally by the ectal origin of the spermathecal diverticula.

M. durendali and *excalaberi* are sympatric and morphologically similar. Nevertheless, each may be recognized on the distribution and separation of the spermathecal pores, separation of the male pores, and arrangement of the genital markings (differences in size and setal numbers are insignificant). The variations in the distinguishing characters are listed in Table 14.

Table 14 Character variation in the *Metapheretima durendali* species-group

Character	*durendali*	*excalaberi*
Spermathecal furrows	4/5/6/7/8 5/6/7/8 6/7/8 6/7	4/5/6
Separation of spermathecal pores	0·22	0·30
Separation of male pores	0·16	0·22
Preclitellar genital markings	*xi, xii*	*ix, xi–xiii*
Postclitellar genital markings	*xvii, xix–xxiii*	*xvii, xix*

Of the five samples examined, *durendali* and *excalaberi* were found together in four in which the proportion of individuals of the two species present varied. It is not possible to establish a correlation between the relative population densities of the species and any of the ecological data. Details of the ecological data and the numbers of specimens collected at each locality are given in Table 15.

Table 15 Proportions of *Metapheretima durendali* and *M. excalaberi* found at various localities

Locality	*excalaberi* (all 4/5/6)	*durendali* (thecal types, 4/5/6/7/8: 6/7/8: 6/7: athecate)
Gentle ridge		
0–15 cm (K440)	13[1]	4 (0: 1[2]: 1: 2)
0–15 cm (K491)	3	11 (10: 0: 0: 1)
Wet gulley		
0–15 cm (K530)	24	21[1] (7: 1: 3: 10)
15–25 cm (K547)	1	0
0–30 cm (K561)	1	26 (26: 0: 0: 0)

[1] Indicate type series.

[2] The spermathecal pores of this individual were in furrows 5/6 (right side only), 6/7 (left side only) and 7/8 (both right and left sides).

Metapheretima excalaberi sp. nov.

DIAGNOSIS. *Metapheretima* with male pores on penes within copulatory pouches; paired spermathecal pores about one third of the body circumference apart in furrows 4/5/6. Holandric.

DESCRIPTION. *External characters.* Length *c.* 38 mm, diameter *c.* 2 mm, *C.* 115 segments. Clitellum *xiv–xvi*. First dorsal pore 11/12. Setae, 40–46 on *vii*, 30–35 on *xx*, setal ring regular (*aa*=*ab*=*yz*=*zz*).

Male pores on short slim penes within shallow copulatory pouches, *c.* 0·22 body circumference apart. Female pore single. Spermathecal pores large, paired in 4/5/6, *c.* 0·30 body circumference apart.

Genital markings (Fig. 42a), large, paired, presetal slightly median to the line of the male pores on *xvii*, *xix*; slightly median to the spermathecal pores on *ix*, *xi–xiii*.

Internal characters. Septa 5/6/7/8 thickened, 8/9 absent, 9/10–13/14 thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs paired, extending to the dorsal line in *x* and *xi*, seminal vesicles paired, extending to the dorsal line in *xi* and *xii*, those of *xi* enclosed in the testes sacs. Pseudoseminal vesicles absent. Spermathecae (Fig. 33f) paired in *v* and *vi*.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 8C, 5A Top 15 cm of alluvial clay derived from gabbro, pH 5·5–6·3, highly humidified, organic content 15–30%, C/N ratio 8–9, gentle ridge with mixed lower montane forest, *Podocarpus*, Eleocarpacae, Lauracae, Cumoniaceae dominant, Bismarck range, Eastern Highland district, Papua New Guinea, 5° 57′ S, 145° 15′ E, rainfall 890 cm/year, altitude 2500 m, *coll* D R Kershaw 14 Jul 1971; BMNH 1976.5.75–87 (syntypes of *excalaberi*). 29C Locality and collector as above; BMNH 1976.5.88–115.

Metapheretima durendali sp. nov.

DIAGNOSIS. *Metapheretima* with male pores on penes within copulatory pouches; paired spermathecal pores about one fifth of the body circumference apart in furrows (4/5/6) 6/7 (7/8). Holandric.

DESCRIPTION. *External characters.* Length *c.* 30 mm, diameter *c.* 2 mm. *C.* 100 segments. Clitellum *xiv–xvi*. First dorsal pore 11/12. Setae 31–43 on *vii*, 35–47 on *xx*, setal ring regular (*aa*=*ab*=*yz*=*zz*).

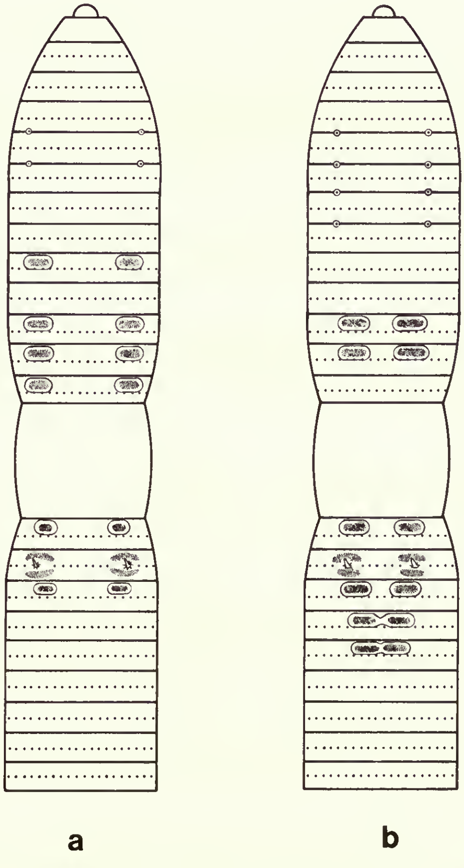

Fig. 42 Anterior ventral surface, diagnostic characters. (a) *Metapheretima excalaberi* sp. nov.; (b) *M. durendali* sp. nov.

Male pores on short, slim penes within shallow copulatory pouches, *c.* 0·16 body circumference apart. Female pore single. Spermathecal pores large, paired in 4/5/6/7/8, rarely 5/6/7/8, 6/7/8 or 6/7, *c.* 0·22 body circumference apart.

Genital markings (Fig. 42b) large paired, presetal slightly median to the line of the male pores on *xvii*, *xix–xxii*; slightly median to the spermathecal pores on *xi*, *xii*.

Internal characters. Septa 5/6–7/8 slightly thickened, 8/9 absent, 9/10–13/14 thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs paired, extending to the dorsal line in *x* and *xi*, seminal vesicles paired, extending to the dorsal line in *xi* and *xii*, those of *xi* enclosed in the testes sacs. Spermathecae (Fig. 33g) paired, usually in *v–viii*, rarely in *vi–viii*, *vii–viii* or *vii* only.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 26C Top 30 cm of soil of alluvial clay derived from gabbro, pH 5·5–6·3, highly humidified, organic content 15–30%, C/N ratio 8–9, wet gully covered with mixed lower montane forest, *Podocarpus*, Eleocarpacae, Lauracae Cumoniaceae dominant, Bismarck range, Eastern Highland district, Papua New Guinea, 5° 57′ S, 145° 15′ E, rainfall 890 cm/year, altitude 2500 m, *coll* D R Kershaw 20 Jul 1971; BMNH 1976.5.30–65 (syntypes of *durendali*). 34C, 2A Data and collector as above; BMNH 1976.5.1–29, 66–74.

Metapheretima oinakensis species-group

DIAGNOSIS. *Metapheretima* with male pores on penes, usually within copulatory pouches; large paired, spermathecal pores in one or two furrows. Spermathecal diverticula simple, ectal in origin. Glandular ridges usually associated with the male pores.

SPECIES INCLUDED. *andurili, dorii, glamdringi, kilii, oinakensis, orcrista, parmata, stingi, tawarinensis.*

DISTRIBUTION. New Guinea.

REMARKS. *M. andurili* may be readily distinguished from the other members of this species-group by the occurrence of the spermathecal pores in furrow 5/6 and occasionally 6/7, instead of in furrow 7/8 only. Marker characters for the recognition of the species with spermathecal pores in furrow 7/8 only are given in Table 16.

Table 16 Marker characters of the members of the *Metapheretima oinakensis* species-group with spermathecal pores in furrow 7/8 only

Species	Separation of spermathecal pores	Copulatory pouches	Glandular ridges	Other genital markings Presetal	Other genital markings Postsetal	Testes
tawarinensis	0·16	absent	*xvii* only	*vii, x, xix, xx*	*xvii*	Holandric
kilii	0·20	absent	?	*xix*	*xvii*	Metandric
dorii	0·37	absent	?	–	*xvii, xix, xxiv*	Metandric
stingi	0·12	present	absent	*xix, xx*	*xvii*	Holandric
oinakensis	0·25	present	absent	*ix–xiii, xvii, xix–xxii*	–	Holandric
orcrista	0·07	present	*xvii–xix*	*x*	–	Holandric
parmata	'closely paired'	?	*xvii–xx*	–	–	Holandric
glamdringi	0·18	present	*xviii* only	*xvii, xix, xx*	*ix*	Proandric

Metapheretima tawarinensis (Cognetti, 1911)

Pheretima tavvarinensis (sic) Cognetti, 1911 : 2.
Pheretima tawarinensis: Cognetti, 1912 : 543.
Metapheretima tawarinensis: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with simple male pores on short penes; large spermathecal pores about one sixth of the body circumference apart in furrow 7/8. Holandric. Spermathecal diverticula simple and ental.

DESCRIPTION. *External characters.* Length 15–130 mm, diameter 1·5–3 mm. 73–121 segments. Clitellum *xiii–xvi*. First dorsal pore 11/12 or 12/13. Setae, 38–82 on *vii*, 34–40 on *xx*, setal ring regular with ventral gaps on postclitellar segments ($aa = 2ab = 2yz = 2zz$).

Male pores on short, stout penes not incorporated in copulatory pouches, *c.* 0·16–0·18 body circumference apart. Female pores paired. Spermathecal pores large in 7/8, *c.* 0·14–0·16 body circumference apart.

Genital markings (Fig. 43a) large, paired presetal on *x* or occasionally *viii*, in line with the spermathecal pores, paired, presetal on *xix*, *xx* and rarely more posterior segments, postsetal on *xvii*, in line with the male pores. The presetal region of *xvii* is elevated to form a ridge similar to that found in *Metapheretima kilii* and *M. dorii*.

Internal characters. Septa 5/6/7/8 slightly thickened, 8/9/10 absent, 10/11/12/13 slightly thickened. Intestine begins in *xv*. Lateral hearts in *x–xiii*.

Holandric, testes sacs small, paired, ventral in *x* and *xi*, seminal vesicles extending to the dorsal line in *xi* and *xii*. Spermathecae (Fig. 33h) paired in *viii*.

DISTRIBUTION. New Guinea.

REMARKS. The descriptions of this species provided by Cognetti (1911, 1912) were based on the examination of a single clitellate specimen 15 mm long which lacked genital markings. Because of the poor condition of the holotype Cognetti was unable to determine the beginning of the intestine, whether the species possessed intestinal caeca, the positions of the lateral hearts or the condition of the anterior male reproductive system. The new specimens have been identified as this species on the basis of the long clitellum, shape of spermathecae and the separation of the male and spermathecal pores.

MATERIAL EXAMINED. *Previously reported.* 1C Tawarin, New Guinea; Amsterdam Vol. 308 (holotype of *tawarinensis*).

New records. 1C, 1A Kaironk valley, Schrader range, Papua New Guinea, 1750 m, *coll* R N H Bulmer; BMNH 1976.2.68–69. 1C, 1A Webag, Western Highlands, Papua New Guinea, *coll* J W Copland; BMNH 1976.3.402–3. 12C Bismarck range, Eastern Highland district, Papua New Guinea, 2500 m, *coll* D R Kershaw 1971; BMNH 1976.5.184–188, 195–204.

Metapheretima kilii sp. nov.

DIAGNOSIS. *Metapheretima* with male pores on penes; large paired spermathecal pores about one fifth of the body circumference apart in furrow 7/8. Metandric. Spermathecal diverticula simple and ental. Male genital field as Fig. 43b.

DESCRIPTION. *External characters.* Length 300 to over 335 mm, diameter 9–10 mm. *C.* 253 segments. Clitellum *xiv–xvi*. First dorsal pore 13/14. Setae, *c.* 265 on *vii*, *c.* 200 on *xx*, setal ring regular on preclitellar segments ($aa = ab = yz = zz$), slightly crowded ventrally on postclitellar segments ($2aa = 2ab = yz = zz$).

Male pores on stout penes *c.* 0·20 body circumference apart. Female pores paired. Spermathecal pores paired, large transverse slits in 7/8, *c.* 0·20 body circumference part.

Genital markings (Fig. 43b) closely paired, postsetal on *xvii*, presetal on *xix*.

Internal characters. Septa 5/6/7/8 thickened, 8/9/10 absent, 10/11–13/14 membranous. Oesophagus with paired, slight dorsolateral pouches in *xi*. Intestine begins in *xvi*. Lateral hearts in *x–xiii*.

Metandric, testes sacs small, paired, spherical, lateromedian in position, in *xi*, seminal vesicles large, reaching the dorsal line in *xii*. Copulatory pouches absent. Spermathecae (Fig. 33i) paired in *viii*.

DISTRIBUTION. New Guinea.

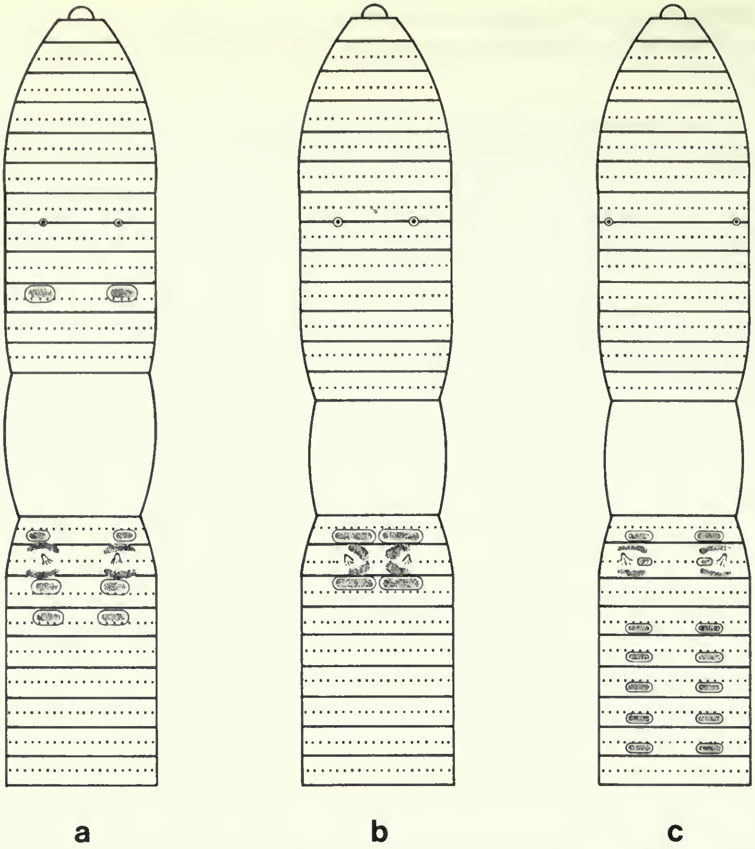

Fig. 43 Anterior ventral surface, diagnostic characters. (a) *Metapheretima tawarinensis*; (b) *M. kilii* sp. nov.; (c) *M. dorii* sp. nov.

MATERIAL EXAMINED. 2C, 1A Moist, dense mixture of peat and soil, very rich in humus, Land Resettlement Scheme (area drained 3 years prior to collection), Kendig, Mt Hagen district, Western Highlands, Papua New Guinea, 5° 48′ S, 144° 26′ E, *coll* J W Copland 15 Nov 1971; BMNH 1976.3.33–35 (syntypes of *kilii*). 31A Dark sandy loam covered by light vegetation, 120–150 m above Nupa village, Bena Bena subdistrict, c 15 miles east of Goroka, Eastern Highlands, Papua New Guinea, *coll* J W Copland 12 Oct 1971; BMNH 1976.3.36–67. 1A Kaironk valley, Schrader range, Madang district, Papua New Guinea, 1750 m, *coll* R N H Bulmer 9 Nov 1973; BMNH 1976.2.70. 3C, 6A Bismarck range, Eastern Highlands, Papua New Guinea, 2500 m, *coll* D R Kershaw 14–20 Jul 1971; BMNH 157–165. 18A Nupa village, Bena Bena subdistrict, *c*. 15 miles east of Goroka, Eastern Highlands, Papua New Guinea, *coll* J W Copland 13 Nov 1971; BMNH 1977.1.15–32. 5A Locality as above, *coll* J W Copland 31 Aug 1971; BMNH 1977.1.33–37.

Metapheretima dorii sp. nov.

DIAGNOSIS. *Metapheretima* with male pores on penes; paired spermathecal pores about one third of the body circumference apart in furrow 7/8. Metandric. Spermathecal diverticula simple and ental. Male genital field as Fig. 43c.

DESCRIPTION. *External characters*. Length *c*. 145, diameter *c*. 6 mm. *C*. 161 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, *c*. 174 on *vii*, *c*. 70 on *xx*, setal ring regular on preclitellar segments ($aa=ab=yz=zz$) with dorsal and ventral gaps on postclitellar segments ($aa=2ab=2yz=zz$).

Male pores on stout penes, *c.* 0·26 body circumference apart. Female pores paired. Spermathecal pores paired, large transverse slits in 7/8, *c.* 0·37 body circumference apart.

Genital markings (Fig. 43c) paired, slightly median to the male pores, postsetal on *xvii*, *xx–xxiv*. Setal on *xviii*.

Internal characters. Septa 5/6/7/8 thick, 8/9 absent, 9/10–13/14 membranous. Oesophagus with slight paired dorsal pouches in *xi*. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs small, spherical paired, lateroventral in position in *xi*, seminal vesicles large, elongate in *xii*. Pseudoseminal vesicles in *xiii*, vestigial, *xiv*, medium sized. Copulatory pouches absent. Spermathecae (Fig. 33j) paired in *viii*.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 3C, 6A Moist dark loam of moderate–high organic content, sloping plot being prepared for Kau Kau, boundary of Wabag, Western Highlands, Papua New Guinea, 5° 28′ S, 143° 40′ E, altitude 2000–3000 m, *coll* J W Copland 16 Nov 1971; BMNH 1976.3.23.31 (syntypes of *dorii*). 1C Data and collector as above; BMNH 1976.3.32.

Metapheretima andurili sp. nov.

DIAGNOSIS. *Metapheretima* with male pores on slim penes within copulatory pouches; large paired spermathecal pores one quarter to two fifths of the body circumference apart in furrow 5/6 and occasionally 6/7. Metandric, spermathecal diverticulum simple and ental in origin.

DESCRIPTION. *External characters.* Length 60–72 mm, diameter 3–4 mm. 64–79 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, 43–56 on *vii*, 40–65 on *xx*, setal ring regular ($aa=ab=yz=zz$).

Male pores on long slim penes within copulatory pouches 0·24–0·29 body circumference apart. Female pore(s) single or paired. Spermathecal pores large, paired in 5/6 and occasionally 6/7, 0·26–0·42 body circumference apart.

Genital markings (Fig. 44a), paired, presetal, median to the spermathecal pores on *vi*, median to the male pores on *xviii*, crescentic markings of *xviii* absent.

Internal characters. Septa 5/6–7/8 slightly thickened, 8/9/10 absent, 10/11–13/14 slightly thickened. Intestine begins in *xv*. Lateral hearts in *x–xii*.

Metandric, testes sacs small, ventral in *xi*, seminal vesicles large, trilobate, reaching the dorsal line in *xii*. Pseudoseminal vesicles vestigial in *xiii* and *xiv*. Copulatory pouches large, spherical invading the coelom of *xviii*, penes long and slender. Spermathecae (Fig. 33k) paired in *vi* and occasionally in *vii*.

DISTRIBUTION. South-east New Guinea.

REMARKS. The individual reported from Mt Suckling differs from the type series by the spermathecal pores being more closely paired, an additional pair of spermathecae opening into furrow 6/7, more numerous setae and the lack of genital markings. The absence of genital markings and the number of setae may be attributed to a different state of maturity but the differences in the spermathecal system may indicate that this specimen represents a separate taxon. In the absence of an adequate series of specimens it is not proposed to recognize these differences taxonomically.

None of the four individuals examined possesses the crescentic markings diagnostic of the genus but the form of the copulatory pouches and penes, spermathecal pores and spermathecal diverticula are consistent with those present in other members of the *Metapheretima oinakensis* species-group.

MATERIAL EXAMINED. 3C Sarari, Milne Bay, Papua New Guinea, 10° 36′ S, 150° 39′ E, *coll* J W Copland 21 Jul 1971; BMNH 1977.1.1–3 (syntypes of *andurili*). 1C Mt Suckling, Papua New Guinea, *coll* W H Ewer Jun 1972; BMNH 1976.4.1.

Metapheretima stingi sp. nov.

DIAGNOSIS. *Metapheretima* with male pores on penes within copulatory pouches; paired spermathecal pores about one eighth of the body circumference apart in furrow 7/8. Holandric. Spermathecal diverticula simple and ental. Male genital field as Fig. 44b.

DESCRIPTION. *External characters.* Length 74–94 mm, diameter *c.* 2 mm. 126–128 segments. Clitellum *xiv–xvi.* First dorsal pore 12/13. Setae, 76–84 on *vii*, *c.* 40 on *xx*, setal ring regular on preclitellar segments (*aa*=*ab*=*yz*=*zz*), with dorsal and ventral gaps on postclitellar segments (*aa*=2*ab*=2*yz*=*zz*).

Male pores on elongate lobate penes within shallow copulatory pouches, *c.* 0·14 body circumference apart. Female pores paired. Spermathecal pores large, paired in 7/8, *c.* 0·12 body circumference apart.

Genital markings (Fig. 44b) single presetal extending beyond the line on the male pores, on *xix* and *xx*, postsetal crescentic markings of *xviii* absent.

Internal characters. Septa 5/6/7/8 thickened, 8/9 membranous, 9/10 absent 10/11/12/13/14 membranous. Intestine begins in *xvi.* Lateral hearts in *x–xii.*

Holandric, testes sacs paired, large with dorsal connections between the members of a pair, enclosing the lateral hearts and in *xi* the seminal vesicles. Seminal vesicles in *xi* small, in *xii* large, extending to the dorsal line. Male pores on elongate penes within coelomic copulatory pouches. Spermathecae (Fig. 33l) paired in *viii.*

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 2C Moist medium to heavy dark loam with considerable organic content, covered by mat of Paspalum, bank of small creek running through no. 12 paddock, Sepik plains Livestock station, Urimo, Wewak, Sepik district, Papua New Guinea, 3° 49′ S, 143° 41′ E, *coll* J W Copland 11 Nov 1971; BMNH 1976.3.11–12 (syntypes of *stingi*). 1C, 1A Data and collector as above; BMNH 1977.1. 151-152 (syntypes of *stingi*).

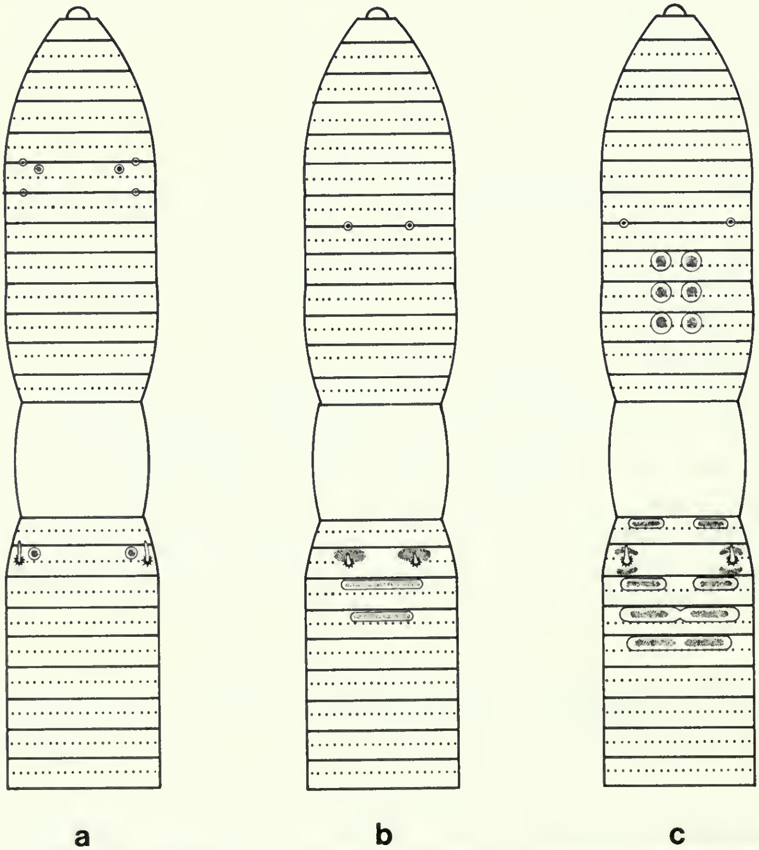

Fig. 44 Anterior ventral surface, diagnostic characters. (a) *Metapheretima andurili* sp. nov.; (b) *M. stingi* sp. nov.; (c) *M. oinakensis.*

Metapheretima oinakensis (Cognetti, 1914)

Pheretima oinakensis Cognetti, 1914 : 355.
Metapheretima oinakensis: Sims & Easton, 1972 : 181, 233.

DIAGNOSIS. *Metapheretima* with male pores on penes within copulatory pouches; paired spermathecal pores about one quarter of the body circumference apart in furrow 7/8. Holandric. Spermathecal diverticula simple and ental. Postclitellar genital field as Fig. 44c.

DESCRIPTION. *External characters.* Length 38–107 mm, diameter 3–4 mm. 90–156 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae 100–120 on *vii*, 30–60 on *xx*, setal ring regular on preclitellar segments ($aa=ab=yz=zz$), with ventral gaps on postclitellar segments ($aa=2ab=2yz=2zz$).

Male pores on slim elongate penes within copulatory pouches, *c.* 0·25 body circumference apart. Female pores paired. Spermathecal pores, large, paired, in 7/8, *c.* 0·25 body circumference apart.

Genital markings (Fig. 44c) paired, presetal on *ix–xiii* median to the line of the spermathecal pores, on *xviii*, *xix–xxii*, median to the line of the male pores.

Internal characters. Septa 5/6/7/8 thickened, 8/9 absent, 9/10–12/13 membranous. Intestine begins in *xv*. Lateral hearts in *ix–xii*.

Holandric, testes sacs small paired, ventral in *x*, paired, extending to the dorsal line in *xi*. Seminal vesicles small, in *ix* enclosed by the testes sacs. Pseudoseminal vesicles small *xiv*. Spermathecae (Fig. 33m) paired in *viii*.

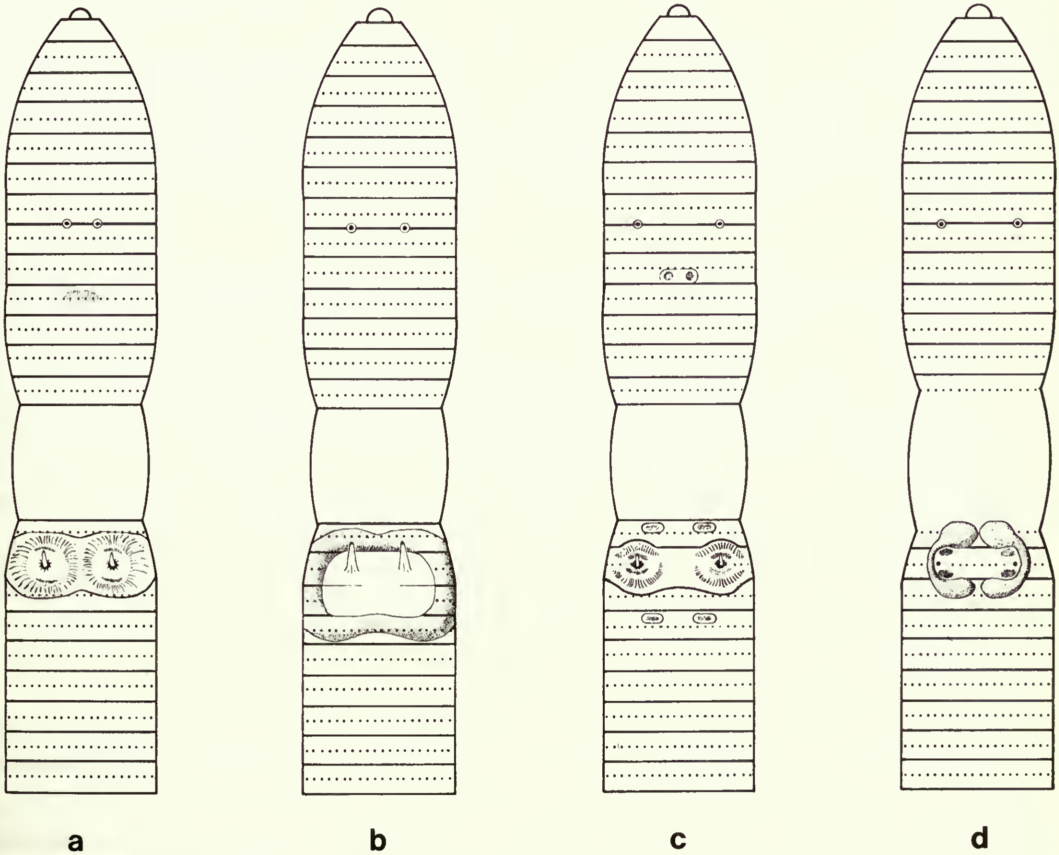

Fig. 45 Anterior ventral surface, diagnostic characters. (a) *Metapheretima orcrista* sp. nov.; (b) *M. parmata*; (c) *M. glamdringi* sp. nov.; (d) *M. jocchana*.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. *Previously reported.* 1C Oinake, New Guinea; Leiden 1838 (holotype of *oinakensis*).
New record. 9C, 1A Moist dark loam of moderate to high organic content, sloping plot being prepared for Kaukau, or boundary of Wabag, Western Highlands, Papua New Guinea, altitude 2000–3000 m, *coll* J W Copland 16 Nov 1971; BMNH 1976.3.1–10.

Metapheretima orcrista sp. nov.

DIAGNOSIS. *Metapheretima* with male pores on elongate penes within copulatory pouches; paired spermathecal pores about one twelfth of the body circumference apart in furrow 7/8. Holandric. Spermathecal diverticula simple and ental. Male pores surrounded by a well-developed glandular ridge (Fig. 45a).

DESCRIPTION. *External characters.* Length 72–95 mm, diameter 2–4 mm. 112–140 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, *c.* 140 on *vii*, *c.* 50 on *xx*, setal ring regular on preclitellar segments ($aa=ab=yz=zz$), with dorsal and ventral gaps on postclitellar segments ($aa=2ab=2yz=zz$).

Male pores on elongate penes within copulatory pouches, *c.* 0·12 body circumference apart. Female pore single. Spermathecal pores large, paired, in 7/8, *c.* 0·07 body circumference apart.

Genital markings (Fig. 45a), single, median, presetal to setal on *x*. Openings of the copulatory pouches are depressed and surrounded by a glandular ridge which occupies *xvii–xix*. This ridge also separates the two pores. On the inner surface of this glandular wall are two pairs of faint, slightly crescentic markings, one pair at 17/18 and the other pair at 19/20, both pairs in line with the male pores.
Internal characters. Septa 5/6/7/8 thickened, 8/9 absent, 9/10 membranous, 10/11 absent, 11/12/13/14 membranous or slightly thickened. Intestine begins in *xvi*. Lateral hearts in *x–xii*.

Holandric, testes sacs paired, small, ventral in *x* and *xi*. Seminal vesicles paired, in *xi* large, in *xii* smaller, both pairs extending to the dorsal line. Male pores on elongate penes within small coelomic copulatory pouches. Spermathecae (Fig. 33n), paired in *viii*.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 5C 15 cm layer of black soil over sandy soil, cultivated for gardens, halfway up hill from creek, Department of Agriculture, Stock and Fisheries Piggery, Goroka, Eastern Highlands, Papua New Guinea, 6° 02′ S, 145° 22′ E, altitude *c.* 3000 m, *coll* J W Copland 13 Oct 1971; BMNH 1976.3.17–21 (syntypes of *orcrista*). 1C Data and collector as above; BMNH 1977.1.42. 2C, 2A DASF Piggery, Goroka, Eastern Highlands, Papua New Guinea, *coll* J W Copland 1 Sep 1971; BMNH 1977.1.38–41. 1C Moist dark loam of moderate to high organic content, sloping plot being prepared for Kaukau, on boundary of Wabag, Western Highlands, Papua New Guinea, *coll* J W Copland; BMNH 1976.3.16. 1C Dark sandy loam covered by light vegetation, 120–150 m above Nupa village, Bena Bena subdistrict, *c.* 24 km east of Goroka, Eastern Highlands, Papua New Guinea, *coll* J W Copland 12 Oct 1971; BMNH 1976.3.22.

Metapheretima parmata (Ude, 1924)

Pheretima parmata Ude, 1924 : 80.
Pheretima (*Pheretima*) *parmata*: Ude, 1932 : 134.
Metapheretima parmata: Sims & Easton, 1972 : 233.

DIAGNOSIS. *Metapheretima* with male pores on slim penes; closely paired spermathecal pores in furrow 7/8. Holandric. Spermathecal diverticula simple ental in origin. Glandular ridges associated with the male pores extending from *xvii* to *xx* (Fig. 45b).

DESCRIPTION. *External characters.* Length *c.* 110 mm, diameter *c.* 3·5 mm. *C.* 180 segments. Clitellum *xiv–xvi*. First dorsal pore 10/11. Setae, 50–65 on *vii*, setal ring with ventral gaps ($aa=2ab$).

Male pores on slim elongate penes originating directly from the body wall, closely paired. Female pores not seen. Spermathecal pores closely paired, in 7/8, in line with the male pores.

Genital markings absent but the male pores are surrounded by a glandular wall extending from *xvii–xx* (Fig. 45b).

Internal characters. Septa 4/5–7/8 thickened, 8/9 absent, 9/10–13/14 membranous. Intestine begins in *xv*. Last heart in *xii*.

Holandric, testes sacs paired, *x*, *xi*, seminal vesicles in *xi* and *xii*. Pseudoseminal vesicles not recorded. Spermathecae paired in *viii*, duct longer than ampulla, diverticulum small, pyriform, ental.

Description after Ude (1924, 1932).

DISTRIBUTION. New Guinea.

REMARKS. This species is known only from the descriptions of Ude (1924, 1932) which are incomplete. Several details of the morphology are unknown, but it is suspected that the spermathecal pores are large as in other species with male pores on penes.

RECORDS. Sepik river (Kaiserin Augusta), Papua New Guinea; Berlin 6474 (type(s) of *parmata*). This series is listed in the catalogue of the Berlin Museum but was lost between 1938 and 1945: Dr Hartwich, personal communication.

Metapheretima glamdringi sp. nov.

DIAGNOSIS. *Metapheretima* with male pores on slim penes within copulatory pouches; paired spermathecal pores about one fifth of the body circumference apart in furrow 7/8. Proandric. Spermathecal diverticula simple ental in origin. Male pores surrounded by glandular ridge restricted to *xviii* (Fig. 45c).

DESCRIPTION. *External characters.* Length 130–138 mm, diameter 4–5 mm. 186–189 segments. Clitellum *xiv–xvi*. First dorsal pore 12/13. Setae, *c*. 190 on *vii*, *c*. 82 on *xx*, setal ring regular although often with displaced setae on preclitellar segments ($aa=ab=yz=zz$), with ventral gaps and no displaced setae on postclitellar segments ($aa=2ab=2yz=2zz$).

Male pores on elongate penes within copulatory pouches, *c*. 0·18 body circumference apart. Female pores paired. Spermathecal pores large, paired, transverse slits, in 7/8, *c*. 0·18 body circumference apart.

Genital markings (Fig. 45c) paired, postsetal on *ix*, paired, presetal on *xvii*, postsetal-intersegmental on *xix–xx*. In addition the male pores are surrounded by a glandular wall similar to that found in *orcrista*.

Internal characters. Septa 5/6/7/8 thick, 8/9 membranous, 9/10 absent, 10/11–13/14 membranous or slightly thickened. Beginning of intestine not seen. Lateral hearts in *x–xii*.

Proandric, testes sacs paired, ventral in *x*, seminal vesicles large, reaching the dorsal line in *xi*. Male pores on penes within small coelomic copulatory pouches. Spermathecae (Fig. 33o) paired in *viii*.

DISTRIBUTION. New Guinea.

MATERIAL EXAMINED. 2C, 1A Dense clay with dense organic matter, covered by thin grass cover, side of road adjacent to coffee plantation, Amahab village, *c*. 16 km west of Maprik, Sepik district, Papua New Guinea, 3° 38′ S, 142° 55′ E, altitude 200–500 m, *coll* J W Copland 12 Nov 1971; BMNH 1976.3.13–15 (syntypes of *glamdringi*).

Metapheretima jocchana (Cognetti, 1911)

Pheretima jocchana Cognetti, 1911 : 5; Cognetti, 1912 : 544; Cognetti, 1914 : 352.
Pheretima (*Pheretima*) *jocchana*: Ude, 1932 : 144; (= ? *kampeni*) Michaelsen, 1938 : 161.
Metapheretima jocchana: Sims & Easton, 1972 : 233, 180.
Pheretima kampeni Cognetti, 1914 : 356.
Metapheretima kampeni: Sims & Easton, 1972 : 233.
Pheretima tumulifaciens Lee, 1967 : 59.
Archipheretima tumulifaciens: Sims & Easton, 1972 : 232.

DIAGNOSIS. *Metapheretima* with large simple male pores; large paired spermathecal pores about one fifth of the body circumference apart in furrow 7/8. Holandric. Spermathecal diverticula small, numerous, ental in origin.

DESCRIPTION. *External characters.* Length 200–600 mm, diameter 6–10 mm. 200–600 segments. Clitellum ½*xiii*–½*xviii*. First dorsal pore 10/11, 11/12, or 12/13. Setae 150–200 on *vii*, 160–180 on *xx*, setal ring regular ($aa = ab = yz = zz$).

Male pores simple, partially invaginated in mature individuals, *c.* 0·30 body circumference apart. Female pores paired, occasionally single. Spermathecal pores large, paired, in 7/8, *c.* 0·20 body circumference apart.

Genital markings (Fig. 45d). In juveniles the markings are paired median to the male pores, postsetal on *xvii*, presetal on *xix*. With maturity the markings enlarge laterally to form a glandular ridge enclosing the male pores.

Internal characters. Septa 5/6–12/13 thickened. Intestine begins in *xvi*. Lateral hearts in *x–xiii*.

Holandric, testes sacs small paired, ventral in *x*, annular in *xi*, seminal vesicles paired, in *xi* enclosed in the testes sacs, and in *xii*. Pseudoseminal vesicles in *xiv*. Spermathecae (Fig. 33p) paired in *viii*.

DISTRIBUTION. New Guinea.

REMARKS. On the basis of the original description, Sims & Easton (1972) placed *tumulifaciens* in the genus *Archipheretima*. Following an examination of the type series *tumulifaciens* is now transferred to *Metapheretima*, and placed in the synonomy of *jocchana*.

MATERIAL EXAMINED. *Previously reported.* 2C Jaga, near lake Sentani, West Irian; Amsterdam Vol 273 (syntypes of *jocchana*). 3C Njao, West Irian; Leiden 1812 (syntypes of *kampeni*). 3A Haripmar village, Sepik valley; Papua New Guinea; Adelaide 940–941 (holotype and paratypes of *tumulifaciens*).

New records. 5A Moist heavy dark soil with a lot of vegetation, holding paddock of AID station, previously a Copra plantation, outskirts of Madang, Madang district, Papua New Guinea, *coll* J W Copland; BMNH 1976.3.68–72. 7A River flats and banks, Sepik livestock station, Urimo, Wewak, Papua New Guinea, *coll* J W Copland 11 Nov; 1971 BMNH 1977.1.9–14.

OTHER RECORDS. New Guinea; Leiden 1851 (*jocchana*: Cognetti, 1914). New Guinea and Berlinhafer, Eilape, New Guinea; Berlin 6476, 6464 (*jocchana*: Ude, 1932). Siwia, New Guinea; Leiden 1852 (*jocchana*: Michaelsen, 1938).

PLEIONOGASTER Michaelsen, 1892

Perichaeta (part): Beddard, 1886 : 298.
Pleionogaster Michaelsen, 1892 : 247; Beddard, 1895 : 433; Michaelsen, 1896 : 198.
Plionogaster: Michaelsen, 1900 : 210; Stephenson, 1930 : 840; Gates, 1943 : 105; Jamieson, 1971*a* : 82.

TYPE SPECIES. *Pleionogaster jagori* Michaelsen, 1892, new designation (non *horsti* Beddard, 1886, invalid designation).

DIAGNOSIS. Megascolecidae with an oesophageal gizzard in *viii* and intestinal gizzards.

DESCRIPTION. As for the only species, *horsti*.

DISTRIBUTION. Philippines, ? Moluccas.

REMARKS. *Pleionogaster* was erected to accommodate two species, *jagori* and *samariensis*, but a type was not designated. Later *Perichaeta horsti* Beddard, 1886 was transferred to the genus and designated as the type species. This designation is invalid (Article 69, Int. Code Zool. Nomencl.) and one of the originally included species, *Pleionogaster jagori* Michaelsen, 1892 (a junior synonym of *horsti*) is here designated as the type of *Pleionogaster*.

The spelling of the name *Pleionogaster* has been the subject of confusion. Michaelsen (1892, 1896) and Beddard (1895) used the correct orthography, *Pleionogaster*, but in 1900 Michaelsen changed the spelling to *Plionogaster*, an unjustified emendation (Article 33, Int. Code Zool.

Nomencl.) which has been used by subsequent authors (Stephenson, 1930, 1933; Gates, 1943; Jamieson, 1971).

Pleionogaster horsti (Beddard, 1886)

Perichaeta horsti Beddard, 1886 : 300.
Pleionogaster horsti: Beddard, 1895 : 434; Michaelsen, 1900 : 211.
Pleionogaster jagori Michaelsen, 1892: 247; Beddard, 1895: 434; Michaelsen, 1900 : 211.
Pleionogaster samariensis Michaelsen, 1892 : 248; Beddard, 1895 : 434; Michaelsen, 1900 : 211.
Pleionogaster ternatae Michaelsen, 1896 : 198; Michaelsen, 1900 : 211.
Pleionogaster sivickisi Stephenson, 1933 : 923.
Pleionogaster sp. Gates, 1943 : 105.

DIAGNOSIS. As for the genus.

DESCRIPTION. *External characters.* Length 50–170 mm, diameter 3–5 mm. 190–270 segments. Body cylindrical, creeping sole absent. Clitellum annular, *xiv–xvii.* First dorsal pore 11/12 or 12/13. Setae perichaetine, 150–200 on *vii*, 70–84 on *xx*, setal ring regular without dorsal or ventral gaps (*aa*=*ab*=*yz*=*zz*).

Male pores simple, large, coincident with the prostate pores, *c.* 0·24 body circumference apart. Female pore single or closely paired, median on *xiv*. Spermathecal pores large, paired, intersegmental in furrows 7/8/9, *c.* 0·23 body circumference apart.

Genital markings (Fig. 46a) paired, in line with the male pores and single median, presetal on *xvi*, *xvii*, *xix*, *xx*, paired, intersegmental, in line with the male pores at 17/18, 18/19.

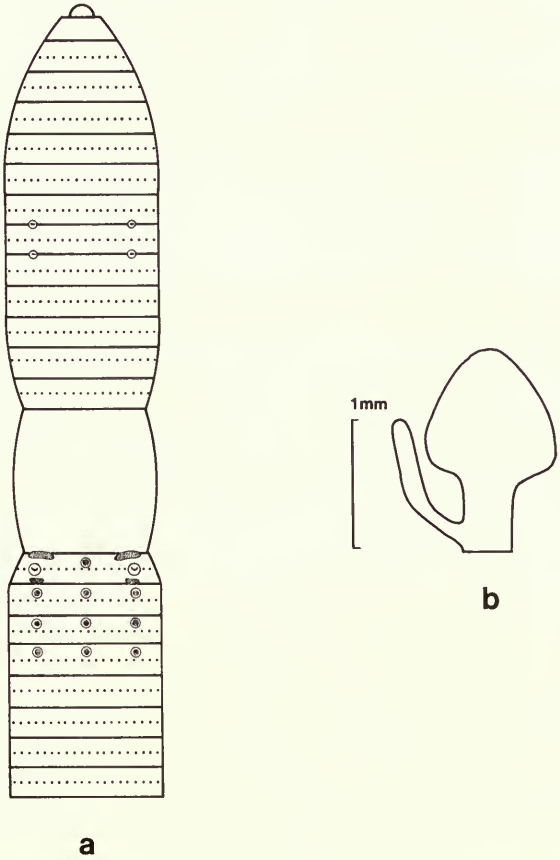

Fig. 46 *Pleionogaster horsti.* (a) Anterior ventral surface, diagnostic characters; (b) spermatheca.

Internal characters. Septa 4/5–8/9 thickened. Poorly developed oesophageal gizzard in *viii.* Oesophagus lacking calciferous glands and dorsal pouches. Intestine begins in *xix* with 3 or 4 gizzards, each *c.* ½ segment in length, in *xxvi, xxvii, xviii* and occasionally *xxix.* Lateral hearts in *x–xiii.*

Holandric, testes sacs single, annular in *x* and *xi,* seminal vesicles small in *xi* and *xii,* enclosed in the testes sacs. One pair of racemose prostates discharging with the male ducts. Ovaries free, paired in *xiii.* Oviducts lead to single or closely paired median equatorial pore(s) on *xiv.* Spermathecae (Fig. 46b) paired in *viii* and *ix.*

DISTRIBUTION. Philippine Islands and possibly the Moluccas.

REMARKS. The taxa assigned to this species vary in the degree of development of the oesophageal gizzard, the number of intestinal gizzards and the number of genital markings. The variation in each of these characters is small and insufficient to justify the recognition of more than a single species.

The reported occurrence of this species in the Moluccas is based on the type of *ternatae* (Michaelsen, 1896). In the original description the type locality was cited as 'Ternate' but later this locality was qualified without explanation as 'Moluken (Ternate)' by Michaelsen (1900 : 211). Since this species has otherwise been reported only from the Philippines, it is uncertain whether this record should be attributed instead to Ternate, Luzon, Philippines and not to Ternate Island, Halmahera.

MATERIAL EXAMINED. 4 micro slides (longitudinal sections), Manila, Luzon, Philippines; BMNH 1974.1.86–89 (syntype of *horsti*). 2C Daraga, Luzon, Philippines; Hamburg v359 (syntypes of *jagori*). 1C 'Ternate' (Halmahera or Philippines ?); Hamburg v3838 (syntype of *ternatae*). 1C, 3A Manila, Luzon, Philippines; BMNH 1930.12.26.5–7 (syntypes if *sivickisi*).

OTHER RECORDS. 1 specimen, Samir Island, Philippines (holotype of *samariensis*). More than 3A Manila, Luzon, Philippines (*Pleionogaster* sp. Gates, 1943).

Species Incertae Sedis

Three species of the *Pheretima* group of genera are known only from individuals with damaged intestines and it is uncertain whether they possess intestinal caeca. They were listed as species *incertae sedis* by Sims & Easton (1972). Descriptions are provided below and the keys of the acaecate genera to which they are potential candidates for inclusion have provision for their recognition.

'Pheretima' cupreae Chen, 1946

Pheretima cupreae Chen, 1946 : 117.
Pheretima cupreae incertae sedis: Sims & Easton, 1972 : 224.

DESCRIPTION. *External characters.* Length *c.* 120 mm, diameter *c.* 6·5 mm. *C.* 95 segments. Clitellum *xiv–xvi.* First dorsal pore 11/12. Setae, *c.* 46 on *iii*, *c.* 52 on *vii*, *c.* 53 on *ix*, *c.* 50 on *xxv*, setal ring with ventral and dorsal gaps ($aa = 1{\cdot}2ab$, $1{\cdot}5\text{–}2yz = zz$).

Male pores on small porophores, *c.* 0·33 body circumference apart. Female pore(s) not recorded. Spermathecal pores small, paired, presetal on *vii* and *viii*, *c.* 0·43 body circumference apart.

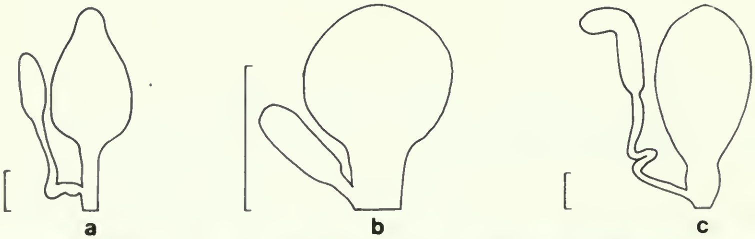

Fig. 47 Spermathecae. (a) *'Pheretima' cupreae*; (b) *'Pheretima' flabellifera*; (c) *'Pheretima' touranensis.* All scales 0·5 mm.

Genital markings (Fig. 48a) paired, pre- and postsetal, slightly median to the spermathecal pores on *vii* and *viii*, single, postsetal, median on *vii* and *viii*, paired, clusters of 3 or 4 papillae slightly median to the male pores on *xviii* and a pair of incomplete glandular walls enclose the male pores anteriorly, laterally and posteriorly.

Internal characters. Septa 5/6–7/8 thickened, 8/9/10 absent, 10/11–12/13 thickened. Intestine begins in *xv*. Lateral hearts not recorded.

Holandric, testes sacs paired in *x* and *xi*, seminal vesicles paired in *xi* and *xii*. Spermathecae (Fig. 47a) in *vii* and *viii*.

Description after Chen (1946).

DISTRIBUTION. Szechwan, China.

REMARKS. The majority of Chinese members of the *Pheretima* group belong to the caecate genera *Amynthas* and *Metaphire* so it is probable that *P. cupreae* possesses intestinal caeca and belongs to the former, *Amynthas*, where it would be accommodated in the *pomellus* species-group. However, *Pheretima cupreae* may be a candidate to two of the acaecate genera, *Polypheretima* and *Metapheretima*. The former, *Polypheretima*, has an indigenous range that comes close to China, but the presence of glandular walls associated with the male pores are reminiscent of the crescentic markings diagnostic of *Metapheretima*.

RECORDS. 1C (damaged) Mt King-Fu, Szechwan, China (holotype of *cupreae*).

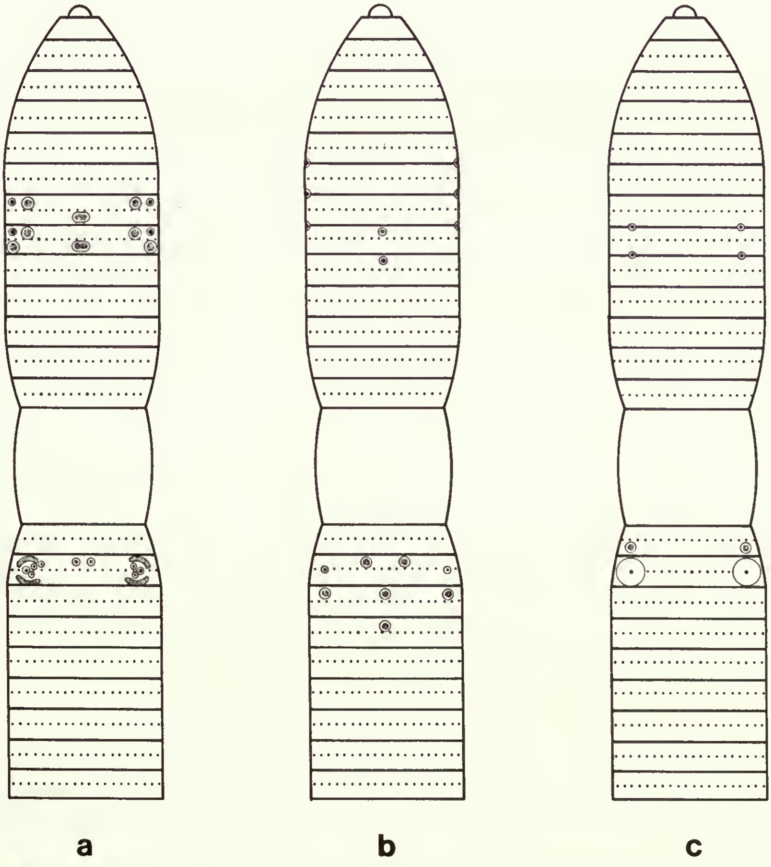

Fig. 48 Anterior ventral surface, diagnostic characters. (a) '*Pheretima*' *cupreae*; (b) '*Pheretima*' *flabellifera*; (c) '*Pheretima*' *touranensis*.

'Pheretima' flabellifera Cognetti, 1911

Pheretima flabellifera Cognetti, 1911 : 2; Cognetti, 1912 : 548.
Pheretima flabellifera incertae sedis: Sims & Easton, 1972 : 224.

DESCRIPTION. *External characters.* Length *c.* 26 mm, diameter *c.* 2·5 mm, *C.* 73 segments. Clitellum *xiv–xvi.* First dorsal pore not recognized. Setae, *c.* 50 on *vii* and *xx*, setal ring with ventral (? and possibly dorsal) gaps ($aa = 1{\cdot}5ab = 1{\cdot}5yz$).

Male pores on circular porophores *c.* 0·35 body circumference apart. Female pore single. Spermathecal pores small, paired, intersegmental in 5/6/7/8, *c.* 0·50 body circumference apart.

Genital markings (Fig. 48b) single, median on *viii* and *ix*, paired, presetal, median to the male pores on *xviii*, paired, presetal, in line with the male pores on *xix*, single median, presetal on *xix* and *xx*.

Internal characters. Anterior septa present and delicate. Intestine begins in *xv*, intestinal caeca ? Lateral hearts in *x–xii*.

Holandric, testes sacs paired, small, ventral in *x* and *xi*, seminal vesicles extending to the dorsal line in *xi* and *xii*. Spermathecae (Fig. 47b) paired in *vi–viii*.

DISTRIBUTION. New Guinea.

REMARKS. Until data about the intestinal caeca become available for this species, it may be considered to be candidate for three genera of the *Pheretima* group of genera, *Amynthas*, *Pithemera* and *Polypheretima*. With intestinal caeca it would be eligible to be included in *Amynthas*, and belong to the *hawayanus* species-group (unknown in the Papuan area) or *Pithemera*. If it should lack caeca, then it would become a member of *Polypheretima* where its affinities would then be with the *bifaria* species-group which is also indigenous in New Guinea.

MATERIAL EXAMINED. 1C Meniheon Geb. West Irian; Amsterdam Vol 254 (holotype of *flabellifera*).

'Pheretima' touranensis Michaelsen, 1934

Pheretima (*Pheretima*) *touranensis* Michaelsen, 1934*c* : 499.
Pheretima touranensis incertae sedis: Sims & Easton, 1972 : 225.

DESCRIPTION. *External characters.* Length 110 mm, diameter 3·5–4 mm. *C.* 90 segments. Clitellum *xiv–xvi.* First dorsal pore not recorded. Setae, *c.* 44 on *v*, *c.* 52 on *ix*, *c.* 56 on *xiii*, setal ring regular without dorsal and ventral gaps ($aa = ab = yz = zz$).

Male pores on large, wart-like papillae which occupy the whole length of the segment, *c.* 0·40 body circumference apart. Female pore(s) not recorded. Spermathecal pores paired, intersegmental in 7/8/9, *c.* 0·28 body circumference apart.

Genital markings (Fig. 48c) paired, postsetal, in line with male pores, on *xvii.*

Internal characters. Septa 6/7/8 slightly thickened, 8/9/10 absent, 10/11–13/14 moderately thickened. Beginning of intestine not recorded, intestinal caeca ? Lateral hearts not recorded.

Holandric, testes sacs small, paired in *x* and *xi*, seminal vesicles large, broad, sack shaped in *xi* and *xii*. Spermathecae (Fig. 47c) paired in *viii* and *ix*.

Description and Fig. 47c after Michaelsen (1934); Fig. 48c is an interpretation of the genital field based on Michaelsen's written description.

DISTRIBUTION. Vietnam.

REMARKS. Until details of the intestinal caeca become available for this species it is considered as a candidate for inclusion in three genera of the *Pheretima* group, *Amynthas*, *Pithemera* and *Polypheretima*. If it should prove to belong to *Polypheretima* then it would be included within the *bifaria* species-group.

RECORDS. 1C (badly macerated) Tourane, Vietnam (holotype of *touranensis*).

Species transferred to caecate genera of the Pheretima group

Two of the species provisionally assigned to *Metapheretima*, one included in *Planapheretima* and four listed as *incertae sedis* by Sims & Easton (1972), are now transferred to *Amynthas* on the basis of the data discussed below.

Perichaeta subquadrangula Grube, 1877. The original description of this species is incomplete and causes doubt whether the taxon should be included within the *Pheretima* group of genera. Examination of the type specimens (Berlin 706) reveal that it belongs to the *Amynthas diffringens* species-group and that it is probably synonomous with *A. diffringens* (Baird, 1869).

Perichaeta pusilla Ude, 1893 (non *Pheretima pusilla* Ohfuchi, 1956) and *Pheretima enchytraeoides* Michaelsen, 1916. The original descriptions lack information regarding the presence or absence of intestinal caeca. Gates (1961 : 298) is of the opinion that they are both synonomous with *Amynthas minimus* (Horst, 1893). The name *A. minimus* has priority; although an exact date of publication cannot be established for Horst's paper a copy was received by the library of the British Museum (Natural History) on 2 August 1893 while Ude's paper was not published until 12 December 1893.

Pheretima monopera Cognetti, 1911. Damage to the intestine in the region of the intestinal caeca of the unique holotype prevented Cognetti from recognizing these structures. Among recent additions to the collections of the British Museum (Natural History) are several individuals of *monopera*. They all possess caeca so the species *monopera* is now transferred to *Amynthas*.

Pheretima liangi Michaelsen, 1922 was assigned to *Metapheretima* by Sims & Easton (1972) since the original description recorded the absence of intestinal caeca. Re-examination of the unique holotype – Leiden 1813 (2 fragments of body wall); Hamburg v9299 (3 spermathecae, pharynx, gizzard and anterior portion of intestine) – revealed that caeca are present but it was not possible to establish in which segment the caeca originate. It is proposed to transfer the taxon to the genus *Amynthas* and include it in the *A. diffringens* species-group – it could possibly be assigned to the *Pithemera pacifica* group; however, it differs from the members of this group by being holandric.

Pheretima petahana Michaelsen, 1934 was tentatively included in *Metapheretima* since Michaelsen noted that it probably lacked intestinal caeca. No further data can be obtained from a re-examination of the unique holotype (Amsterdam Vol. 293) since all internal structures have been removed. However, a short series of specimens (Stockholm 462) contain three clitellate individuals assignable to this species on external characters. Since these specimens have intestinal caeca originating in *xxvii*, the species is now transferred to *Amynthas* where it is included in the *A. aeruginosus* species-group.

Pheretima hirudinaria Gates, 1958 was assigned to *Planapheretima* by Sims & Easton (1972) since the original description recorded crowded ventral setae and a depressed body. Examination of the unique holotype – New York 7283 – revealed that the body was only slightly depressed, possibly a result of the fixation technique employed, and the setae were not crowded ventrally. In the absence of the generic characters of *Planapheretima* the species has been transferred to *Amynthas* where it is accommodated in the *A. diffringens* species-group. Gates (1958) was only able to detect a single lateral caecum on the left side of the holotype. Re-examination of the holotype revealed that a caecum was present on the right-hand side of the intestine although it was not as well developed as that on the left-hand side.

Several species were omitted from the numerical studies of Sims & Easton (1972) or have been described since in the genus *Pheretima*. They are assigned to the following genera:

Amynthas

A. areniphilus (Chen & Hsü, 1975: 91) (cf. *A. rubellus*).
A. geojeisulae (Song & Paik, 1970*a* : 11) (*A. morrisi* species-group).
A. gucheonensis (Song & Paik, 1970*b* : 105) (*A. tokioensis* species-group).
A. heterogens (Chen & Hsü, 1975: 96) (*A. sieboldi* species-group).
A. jiriensis (Song & Paik, 1971 : 193) (*A. tokioensis* species-group).
A. loti (Chen & Hsü, 1975: 93) (*A. sieboldi* species-group).
A. mediocus (Chen & Hsü, 1975: 92) (*A. diffringens* species-group).
A. nanulus (Chen & Yang, 1975: 89) (*A. morrisi* species-group).

A. seungpanensis (Song & Paik, 1970*a* : 11) (*A. canaliculatus* species-group).
A. tschiliensis kokoanus (Chen & Fang, 1975: 94) (*A. sieboldi* species-group).
Metaphire
M. cruroides (Chen & Hsü, 1975: 93) (*M. houletti* species-group).
M. yapensis (Ohfuchi, 1941 : 283) (*M. houletti* species-group).
Pithemera
P. aimerikiensis (Ohfuchi, 1941 : 302) (*P. bicinta* species-group).
P. eldoni (Gates, 1975 : 6).
P. mira (Gates, 1972*b* : 121) (*P. sedgwicki* species-group).
P. palaoensis (Ohfuchi, 1941 : 287).

Acknowledgements

For donating material to the British Museum (Natural History) I must express my grateful thanks to: Dr R. N. H. Bulmer, Department of Anthropology and Sociology, University of Papua New Guinea (present address: University of Auckland); Dr J. W. Copland, Veterinary Laboratory, Department of Agriculture, Stock and Fisheries, Boroko, Papua New Guinea (present address: Department of Agriculture, Benalla, Victoria); Dr W. H. Ewers, Biology Department, University of Papua New Guinea (present address: Warrnambool Institute of Advanced Education, Victoria); Dr M. Griffiths, Australian National University, Canberra; Dr D. R. Kershaw, Department of Zoology and Comparative Physiology, Queen Mary College, University of London; Mr N. T. Talbot, Veterinary Laboratory, Department of Agriculture, Stock and Fisheries, Boroko, Papua New Guinea and Mrs M. T. C. Wright, Malayan Tobacco Company, Kelantan, Malaysia. For the loan of material I must record my gratitude to: Dr D. M. Devany, Bernice P. Bishop Museum, Honolulu; Professor Dr M. Dzwillo, Zoologisches Institut und Zoologisches Museum, Universität Hamburg; Dr G. Hartwich, Museum für Naturkunde an der Humboldt-Universität zu Berlin; Dr S. Kadarsan, Museum Zoologicum Bogoriense, Bogor; Dr E. Kirsteuer, The American Museum of Natural History, New York; Dr J. van der Land, Rijsmuseum van Natuurlijke Historie, Leiden; Dr H. Laws, South Australian Museum, Adelaide; Dr R. Oleröd, Naturhistoriska Riksmuseet, Stockholm; Dr M. Sarica, Museo ed Instituto di Zoologica Systematica, Università di Torino; Dr S. van der Spoel, Zöologisch Museum, Universitat van Amsterdam; Dr V. Stemberger, Naturhistorisches Museum Wein, Vienna and Dr E. Tortonese, Museo Civico di Storia Naturale 'Giacomo Doria', Genoa.

For information about their collections I am grateful to: Dr G. L. Alcasid, Pambansung Museo, Manila; Dr R. Alvardo, Museo Nacional de Ciencias Naturales, Madrid; Dr P. Hitchings, The Australian Museum, Sydney; Dr M. Imajima, The National Science Museum, Tokyo and Dr J. B. Kirkegaard, Universitetets Zoologiske Museum, Copenhagen. I would like to thank Dr B. G. M. Jamieson, University of Queensland, for examining the type series of *Metapheretima bulmeri* in the Australian Museum. I am especially grateful to Mr R. W. Sims for his advice and encouragement during the preparation of this report and for reading the manuscript. Finally, I would like to thank Miss K. M. Shaw for her advice and making available her computer programs and Mr D. W. Cooper for preparing the microslides for the morphological studies.

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Bulletin of the British Museum (Natural History)

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Zoology series Vol 35 No 2 26 April 1979

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World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

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ISSN 0007-1498

Zoology series
Vol 35 No 2 pp 127–200

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 26 April 1979

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The dargyrome of the genus *Euplotes* (Hypotrichida, Ciliophora)

Michael A. Gates and Colin R. Curds

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Introduction

Since the advent of silver impregnation (Chatton & Lwoff, 1930) to reveal the infraciliature of ciliated protozoa, several previously undetected cortical characteristics have been postulated to be of taxonomic value. Tuffrau (1960) was the first worker to apply silver-staining techniques to hypotrich ciliates of the genus *Euplotes* Ehrenberg, 1831,* concentrating mainly on the prominent ventral ciliature. However, he also revealed the pattern of the fibrillar network of silver-lines that covers both the ventral and dorsal surfaces, introducing the term argyrome to describe the totality of this feature, now known to mark the boundaries between adjacent subpellicular vacuoles (Ruffolo, 1976*a*, 1976*b*). Tuffrau classified the dorsal argyrome (hereafter, dargyrome) patterns into three distinct types, and he applied this classification towards the resolution of taxonomic problems involving several large, common and popular freshwater species. In particular, Tuffrau (1960) suggested that *E. patella* (Müller, 1773) Ehrenberg, 1838 could be distinguished from *E. eurystomus* (Wrzesniowski, 1870) Kahl, 1932 by distinct differences in their dargyrome patterns.

On the basis of a retrospective study of the genus, incorporating many taxonomic descriptions that had accumulated since the introduction of silver-impregnation techniques, Curds (1975) presented a refinement of Tuffrau's (1960) dargyrome classification, raising the number of types to six (Fig. 1). Tuffrau's original classification was based essentially on the number of rows of silver-staining polygons (corresponding to subpellicular vacuoles) that occur between any two adjacent kineties (rows of cilia). In Tuffrau's 'vannus' dargyrome type, there is only a single row (as in *E. vannus* (Müller, 1786) Minkjewicz, 1901), while in his 'eurystomus' type, there are two rows, separated by an interkinetal vacuolar boundary. Curds (1975) retained the 'vannus' type, rechristening it 'single-vannus' (Fig. 1a), but he subdivided the 'eurystomus' type into three distinct patterns, depending on the position of the interkinetal boundary. In the 'double-eurystomus' type (Fig. 1b), that boundary is centrally situated, while in the two 'double-patella' types (Figs 1c, 1d), it is displaced to either the left or the right, respectively. The classical species *E. eurystomus* possesses the 'double-eurystomus' dargyrome, while *E. patella* possesses the first variant (Fig. 1c) of the 'double-patella' dargyrome. Tuffrau's 'muscicola' dargyrome type was considered by Curds to consist in a heterogeneous mixture of two types: the 'multiple' dargyrome (Fig. 1e), in which there are several rows of polygons between kineties (as in *E. muscicola* Kahl, 1932), and the 'complex' dargyrome (Fig. 1f), in which the interkinetal space is irregularly subdivided (as in *E. elegans* Kahl, 1932).

The ramifications of this typology are not without consequence to the taxonomy of the genus. Dargyrome pattern is one of the few classical taxonomic attributes still considered to be invariant within species of the genus (Carter, 1972; Curds, 1975; Hill & Reilly, 1976) and it remains, for example, one of the major distinguishing features applicable to the confusing assemblage of common freshwater species which includes, in addition to the classical *E. patella* and *E. eurystomus*, others such as *E. aediculatus* Pierson, 1943, *E. plumipes* Stokes, 1884, *E. variabilis* Stokes, 1887 and *E. woodruffi* Gaw, 1939 (Pierson, 1943; Tuffrau, 1960; Pierson *et al.*, 1968; Carter, 1972; Curds, 1975; Hill & Reilly, 1976; Curds, 1977). All of these species are of cirrotype-9

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* It should be noted that contrary to the publications of several recent authors, the valid date of publication for the genus *Euplotes* is 1831 (see Ehrenberg, 1831 : 12) not 1830 nor 1838. Furthermore, the 1830 date refers to the nominal publication date of the name *Euploea* for which the correct citation, according to Article 21 of the International Code of Zoological Nomenclature should be *Euploea* Ehrenberg, 1832.

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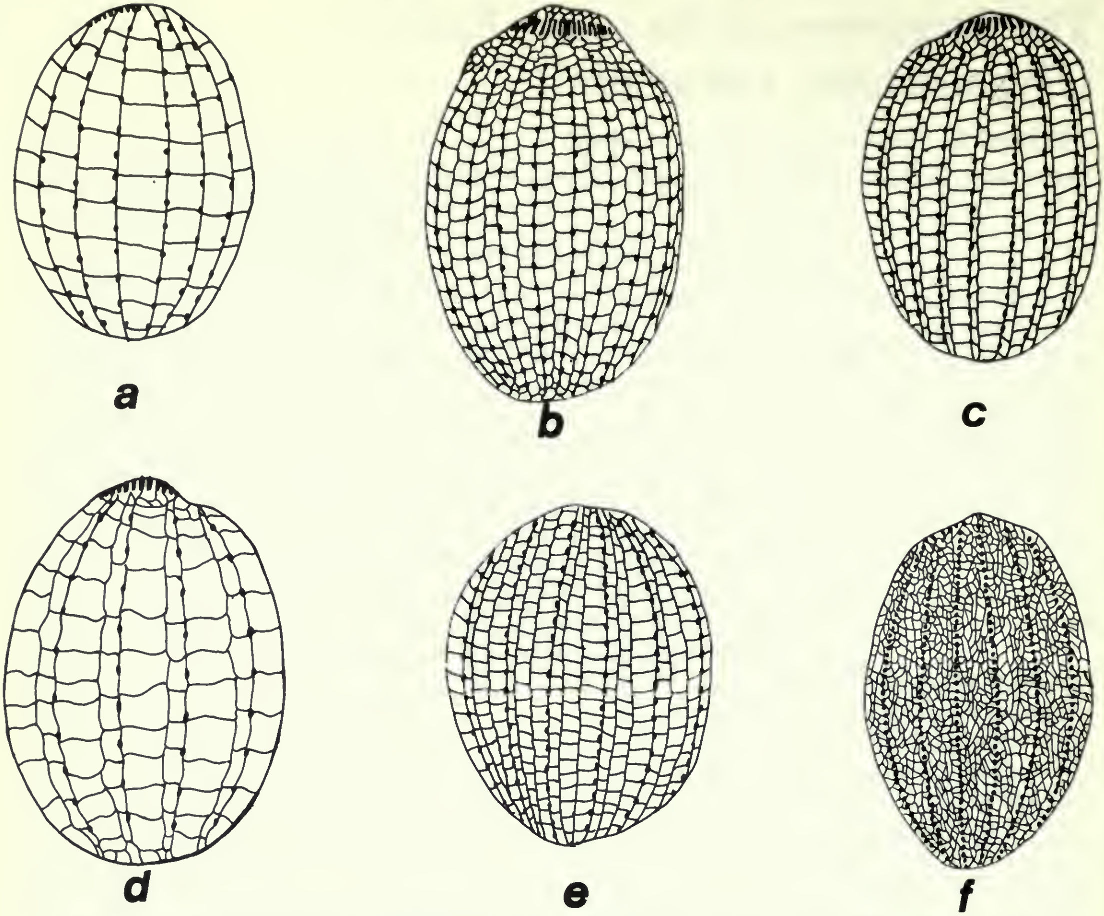

Fig. 1 Dargyrome patterns of *Euplotes*: (a) single-vannus type; (b) double-eurystomus type; (c–d) double-patella types; (e) multiple type; (f) complex type.

(i.e. they have 9 frontoventral cirri), and all of them have very similar cirral patterns on their ventral surface (Gates, 1976).

This paper demonstrates that the subclassification of double dargyromes according to whether the interkinetal boundary is central (the 'double-eurystomus' type) or displaced to the right or left (the 'double-patella' type) is invalid.

Materials and Methods

In March 1975, a clonal population was established in Toronto, Ontario, Canada, of a double dargyrome, cirrotype-10 marine form, labelled QVANNQ (Gates, 1976), which was collected in 1974 from the North Sea off the coast of Denmark and cultured at the British Museum (Natural History). In April 1976, three subclones (1, 2, 3) of this clone were established at the latter institution, and these were sampled at three separate times: A, 11 August 1976; B, 7 December 1976; C, 12 January 1977. These nine samples were silver-stained by a modification of the Chatton–Lwoff procedure (Chatton & Lwoff, 1930; Corliss, 1953; Frankel & Heckmann, 1968).

Within the same microscope slide of a silver-stained preparation of subclonal sample B-1, for example, are found not only typical 'double-eurystomus' specimens (Fig. 2), which are in the majority, but also occasionally a typical 'double-patella' specimen (Fig. 3), plus all of the inter-

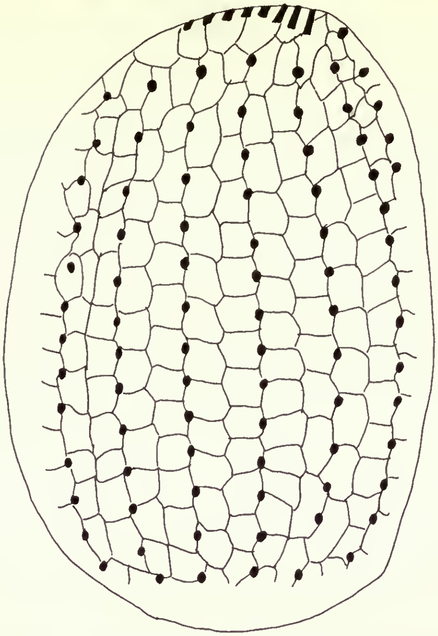

Fig. 2 Dargyrome of a specimen of subclone B-1 of the marine cirrotype-10 *Euplotes* sample, QVANNQ, showing a classical 'double-eurystomus' type of dargyrome.

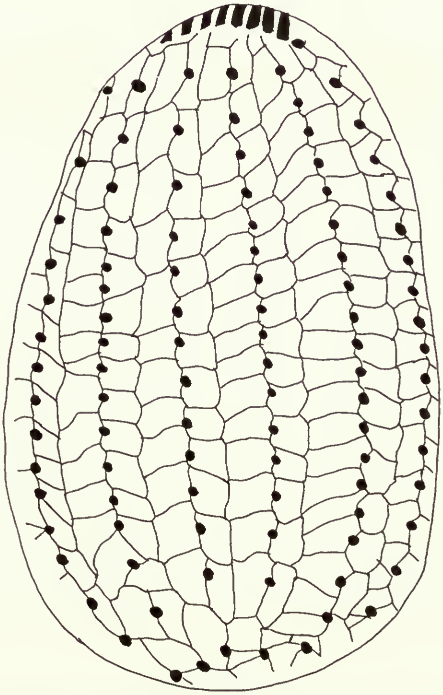

Fig. 3 Dargyrome of another specimen of subclone B-1 from the same slide preparation, showing a classical 'double-patella' type of dargyrome.

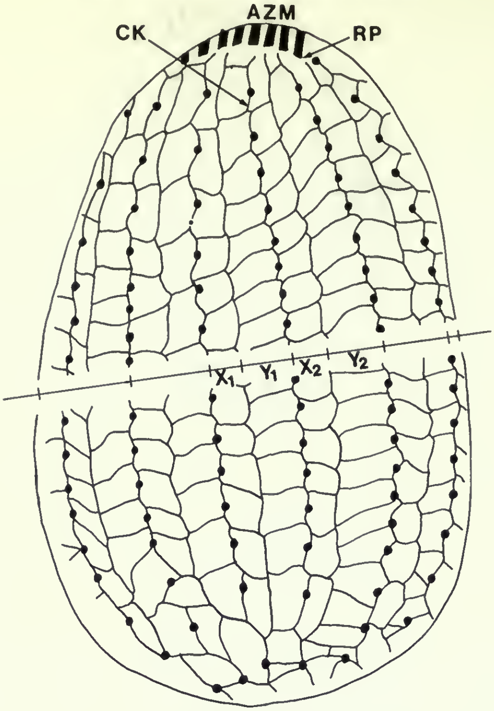

Fig. 4 Diagram of the dorsal surface of a specimen of the QVANNQ *Euplotes* sample, illustrating the measurement transect that provides the two sets of interkinetal distances (x_1, y_1 and x_2, y_2) on either side of the central kinety (ck) that are used to obtain the interkinetal ratios, x_1/y_1 and x_2/y_2, whose average provides a measure of dargyrome type for the specimen. The dorsal origin of the adoral zone of membranelles (AZM) is also shown at the anterior of the specimen, the reference point is indicated by RP.

mediate types. While these examples are suggestive, they are not, in themselves, sufficient to establish the invalidity of a typology. Since evolution is the partitioning of variation, and as variation is quantitative in nature, a detailed quantitative analysis is essential.

As inspection of either Fig. 2 or Fig. 3 reveals, the position of the interkinetal boundary varies with the region of the dorsal surface examined. To obtain an objective, repeatable measure of the position of that boundary within a given population of a double-dargyrome *Euplotes* species, attention must be focused on a restricted portion of the middle of the dorsal surface of well-stained and properly-oriented specimens. The origin of the adoral zone of membranelles (AZM) provides a well-defined reference point (see Fig. 4) on the dorsal surface of this species of *Euplotes*. This point can be used to locate and define the central kinety which is the second kinety lying to the left of the reference point. Accordingly, the widths of the two interkinetal boundaries were measured on either side of the central kinety midway along each specimen.

Using a Leitz Laborlux microscope with 100× oil immersion objective and 10× oculars equipped with a 1·25× drawing tube, the images of the points illustrated in Fig. 4 were recorded on acetate sheets with indian-ink and these were then projected onto millimetre-ruled linear graph paper by means of a Leitz Diascriptor 4 projector. From these coordinate data, the two sets of interkinetal distances (x_1, y_1 and x_2, y_2) determined by the placement of the two central interkinetal boundaries were calculated and the ratios x_1/y_1 and x_2/y_2 formed. Each of these ratios measures the placement of the interkinetal boundary on either side of the central kinety, and their average provides a quantitative measure of the dargyrome of the specimen. Thus, the nature of the dargyrome on each specimen is represented by a single number, the average interkinetal ratio. To measure the dargyrome type of any given population, the mean interkinetal ratio (MIR) is calculated, based on 50 specimens for each sample, except series A-1, where only 19 specimens were available.

Comparisons among populations were made by means of standard analysis of variance tests, primarily the *F*-ratio test (Sokal & Rohlf, 1969). A 95% confidence level was used throughout. Conclusions were not affected by assuming that the average interkinetal ratio is normally distributed within each population (as was verified to be true in one sample): use of the arcsine transformation for ratios (Sokal & Rohlf, 1969) gave similar results to those presented here, which are based on untransformed data. To facilitate comparisons, results are given in terms of the 95% confidence intervals (on either side of the mean) for each sample, based on *t*-values, rather than the *F*-ratios for each group of samples.

Results

An essential ingredient in any quantitative analysis of variation is an examination of the inherent errors of measurement. Table 1 presents the results of measuring the same specimen 50 times, which gives a measurement error confidence interval for the MIR in the order of 0·015. Also shown are the results of measuring 50 specimens of each of two separate slide preparations of the B-1 sample; it is clear that there are no differences among subsamples of this sample. These results demonstrate, respectively, the precision and accuracy of the MIR as a measure of dargyrome type.

Table 1 Error analysis for the mean interkinetal ratio. Using the B-1 subclone, the same specimen was remeasured 50 times to assess the inherent error of measurement. To judge the accuracy of measurement, 50 specimens on each of two separate slides of this same subclone were measured. In this and the two following tables, the mean ($\bar{x}$), standard deviation (*s*) and 95% confidence interval (*c.i.*) are presented

	$\bar{x}$	*s*	*c.i.*
50 replicates	1·0546	0·0505	0·0144
Slide 1	1·0099	0·0972	0·0276
Slide 2	0·9906	0·0990	0·0281

As Figs 2 and 3 clearly illustrate, there can be considerable variation from individual to individual in dargyrome type. But to demonstrate the invalidity of the concept, it must be established that populations of individuals differ, not merely that individuals vary. Given the mean interkinetal ratio of a population, it must be established, first, that the ratio is inherited, and second, that it is sufficiently variable that different subclones may have significantly different ratios. That is, if two individuals are derived from a parental clonal population, are their ratios different, and will those ratios be inherited by their asexual progeny ?

Tables 2 and 3 present the results. For each clone, there are no significant differences in the MIR with time, over the period sampled (Table 2). This demonstrates that the MIR is inherited within clones. If the results are regrouped by fixation date (Table 3), it is apparent that significant differences do exist among the three clones. Clone 1 is always larger in MIR than clone 3, and clone 2 is always intermediate; the differences between clone 1 and clone 3 are significant at the last two fixation times, B and C. This consistent and significant trend shows that different subclones may possess significantly different ratios.

Discussion

The results demonstrate that, although the asexual progeny of an individual inherits the dargyrome type of the parent, different individuals may give rise to progeny which have significantly

Table 2 Mean interkinetal ratios for the 9 subclones, arranged by clone. For each clone, there are no significant differences among the three different sampling times (A, B, C)

Clone	$\bar{x}$	*s*	*c.i.*
A-1	0·9790	0·1657	0·0471
B-1	1·0099	0·0972	0·0276
C-1	1·0760	0·1629	0·0463
A-2	0·9485	0·1525	0·0433
B-2	0·9527	0·1074	0·0305
C-2	0·9977	0·1837	0·0522
A-3	0·9194	0·1471	0·0418
B-3	0·9072	0·1189	0·0338
C-3	0·9477	0·1695	0·0482

Table 3 Mean interkinetal ratios for the 9 subclones, arranged by sampling time. Significantly different clones within each sampling time are indicated by asterisks on the means

Clone	$\bar{x}$	*c.i.*
A-1	0·9790	0·0471
A-2	0·9485	0·0433
A-3	0·9194	0·0418
B-1	1·0099*	0·0276
B-2	0·9527	0·0305
B-3	0·9072*	0·0338
C-1	1·0760*	0·0463
C-2	0·9977	0·0522
C-3	0·9477*	0·0482

different dargyrome types, as measured by the MIR. This form of quantitative uniparental inheritance of the mean interkinetal ratio makes its use as a taxonomic criterion invalid. More poignantly, qualitative distinctions based on the same principle are likewise invalid: the 'double-eurystomus' and 'double-patella' dargyrome types do not exist as separate entities. They represent extremes of a continuum of interkinetal ratios that exists within most large populations of double dargyrome *Euplotes*. The typological fixation of the extremes of this continuum is to be deplored.

The work of Frankel (1973, 1975) demonstrates the considerable independence of the ventral and dorsal surfaces of *Euplotes*. In another marine cirrotype-10 species, *E. minuta* Yocom, 1930, the distribution of ciliary units over the dorsal surface is stable, but there can be large variations both in the number of kineties and in the number of cilia per kinety, while on the ventral surface, the number of frontoventral cirri (the cirrotype) remains constant, even in a basal-body deficient mutant. The present study is also based on a marine cirrotype-10 form, and the most parsimonious interpretation of our results is that other double dargyrome *Euplotes* do have a similar quantitative uniparental inheritance of the MIR. In particular, we suggest that it applies equally well to the cirrotype-9 freshwater forms such as *E. patella* and *E. eurystomus*, which display similar inidvidual variations in MIR (Gates, unpublished observations). In conjunction with the results of quantitative studies of the ventral cirral patterns of these forms (Gates, 1976), such an interpretation is of obvious applicability to the alleviation of the taxonomic confusion which exists among freshwater cirrotype-9 *Euplotes* (see, for example, Curds, 1975; Hill & Reilly, 1976).

The existence of individual variation in dargyrome type is not confined to samples of *Euplotes* having double dargyromes (Gates, 1976, and unpublished observations). Among individuals of various single dargyrome forms, one may see not only the erratic 'reorganizing' dargyromes which Tuffrau (1960) noted in his *E. mutabilis* Tuffrau, 1960, now known to be fully interfertile with *E. crassus* (Dujardin, 1841) Kahl, 1932 (Génermont *et al.*, 1976), but also occasional regions in which a double dargyrome pattern is present, or in which the interkinetal space is further subdivided. The latter phenomenon also occurs in various double dargyrome samples, including *E. harpa* Stein, 1859. Indeed, among some double dargyrome forms, multiple or complex patterns occur in restricted regions of the dorsal surface of a few individuals, while in *E. moebiusi* Kahl, 1932 (Curds, 1974) and *E. tegulatus* Tuffrau, 1960 (Tuffrau, 1960) there is a more general complication of the dargyrome in all specimens examined. Finally, some 'multiple' dargyrome clonal samples yield a few specimens having classical 'complex' dargyromes, suggesting that the latter type is only a variant of the former.

While all of these variants and exceptions are rare, they are as suggestive as Figs 2 and 3. Indeed, they suggest that dargyrome types are not immutable, and that it is possible to suggest an evolutionary sequence from 'single' through 'double' to 'multiple' (with its variant, 'complex') dargyromes (Gates, 1976). That is, the direction of evolutionary change has been the further subdivision of the interkinetal space by the corresponding polymerization of subpellicular vacuoles (see Polyjansky & Raikov, 1976).

The 'single' dargyrome occurs only in small to medium-sized marine species of cirrotype-10, and these forms have identical cirral patterns (Gates, 1976). The 'double' dargyrome is the most common type, found in both marine and freshwater forms of all cirrotypes; it occurs among species with a variety of cirral patterns and sizes; and it is the most variable dargyrome. The 'multiple' and 'complex' dargyromes are restricted to only a few species (Curds, 1975).

The common occurrence and the variable nature of the 'double' dargyrome has led to the creation of subcategories which were presumed by taxonomists to be stable within 'species' (Curds, 1975). Our results demonstrate the invalidity of the subdivision using this type of dargyrome. Although descriptive of particular clones, the 'double-patella', 'double-eurystomus' and 'complex' distinctions, should not be used in assessing taxonomic affinities. Because of the quantitative uniparental inheritance of dargyrome type, these categories are not descriptive of populations of *Euplotes*, even over short periods of time. Accordingly, we propose to modify Tuffrau's (1960) original classification along the more descriptive lines suggested by Curds (1975). The dargyrome of *Euplotes* should be classified as either 'single', 'double' or 'multiple'.

Acknowledgements

The senior author is grateful to the National Research Council of Canada for financial support through a Postdoctorate Fellowship, and to the Trustees of the British Museum (Natural History) and of the Culture Centre of Algae and Protozoa for providing research facilities and space.

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Manuscript accepted for publication 5 January, 1978

A redescription of types of six species of Neotropical Veronicellidae (Mollusca; Gastropoda) in the British Museum (Natural History)*

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Resumo

Com base no exame dos exemplares tipos depositados nas coleções do Museu Britânico de História Natural, Londres, Inglaterra, são redescritas, destacando-se os característicos específicos válidos, as seguintes espécies: *Vaginula cordillerae* Simroth, 1914, *Vaginula fusca* Heynemann, 1885, *Veronicella laevis* Blainville, 1817, *Vaginula nesiotis* Simroth, 1914 e *Vaginula nigra* Heynemann, 1885, bem como um paralectótipo de *Vaginula columbiana* Simroth, 1914.

Introduction

This publication is part four of a series in which the types of neotropical Veronicellidae are redescribed; three parts have already been published (Thomé, 1969*a*, 1969*b*, 1970). Types of six species in the British Museum (Natural History) are considered here and some new features of the external and internal morphology are described. It is the opinion of the author that these characters are important for the correct diagnosis of these species and a full discussion of their significance can be found in Thomé (1969*a*).

Vaginula cordillerae Simroth

Vaginula cordillerae Simroth, 1914 : 303–305, pl. 12, figs 50–53.
Cylindrocaulus fuhrmanni Hoffmann, 1925 : 237 (*partim*), *non* Simroth.

HOLOTYPE. BM(NH) Reg. No. 1928.8.27.26.

TYPE LOCALITY. 'Argelia Cafetal' (east mountain ridge), Columbia – at 1600 m.

LEG. Dr O. Fuhrmann (no date).

The specimen was in good condition; it had been opened longitudinally along the dorsal surface, but all the organs remaining *in situ*.

EXTERNAL MORPHOLOGY (Pl. 1, figs 1–3)
Size. Length: 59 mm; breadth: 19 mm; height: 12 mm; right hyponoyum width: 7·4 mm; sole width: 6·2 mm: distance of female opening from anterior end: 32 mm, from posterior end: 23 mm, from pedal groove: 2·3 mm.
Description. Animal medium size, with a greater width than height; outline elliptical in dorsal view and specimen not arched. Notum dark grey with light brown shading; darker spots correspond to the position of mucous pores. Perinotum light brown, conspicuous, sharpened and slightly upturned. Hyponota grey, as the notum, and devoid of dark spots. Sole light brown without median line. Position of the female opening is about 1/3 of the hyponotum from pedal groove and slightly posterior to the mid-point of the body length. Circular anus situated to the right of sagittal plane and extending a little beyond the pedal groove; closed by a small thick plate, and completely covered by the posterior extension of the foot. This extension is devoid of pigmentation. Simroth (1914) describes coloration as follows: 'Der ganze Ton ist mit Ausnahme der blassen

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* Contribution No. 4, in series 'Redescription of types of Neotropical Veronicellidae (Mollusca; Gastropoda)'.

Bull. Br. Mus. nat. Hist. (Zool.) **35** (2): 127–200 Issued 26 April, 1979

Sohle schwärzlich chocoladen-braun, durchaus einfarbig, kaum dass das Perinotum eine Spur heller bleibt. Hie und da ist auf dem Notum eine hellere ockerige rundliche Stelle von höchstens 1 mm Durchmesser mit einem schwarzen Punkt in der Mitte, einem Drüsentuberkel. Sonst ohne Abzeichen. Das Hyponotum das vom Pigment bis zur Grenze an der Fussrinne gleichmässig bedeckt ist, erscheint ganz feinkörnig. Ebenso das Notum, nur dass sich hier in regelmässigen Abständen von ca. 1 mm deutlich etwas grössere rundliche Körner erheben, die als dunkle Punkte hervortreten, ohne doch tief schwarz zu sein.'

INTERNAL MORPHOLOGY (Figs 1–3, 15)
Digestive system. Anterior intestinal loop covered by a lobe of the digestive gland, which is 4·0 mm wide. Rectum penetrating body wall near the oviduct and above it (Fig. 2).
Nervous system. The pedal nerves originate close together and extend in this manner for half the length of the animal; then they diverge but continue parallel to the posterior end. The pedal nerves are not attached to the body wall until they reach the aorta. Total length of pedal nerves: 35·0 mm; diverge for 20·0 mm; maximum distance separating the parallel nerves: 2·0 mm; meeting aorta at 8·5 mm.
Pedal gland. Cylindrical, flattened, loose and coloured light yellow. Appears to be disproportionally long for the size of the animal. Outside zone clearly delimited up to the distal end, where delimitation is lost. At distal end, inner zone of the gland with a narrow longitudinal furrow. Length in natural position: 16·5 mm; distended: 18·0 mm; width: 1·7 mm (Fig. 1).
Reproductive system. Spermatheca pear-shaped, attached at the swollen end to a thick and well-developed duct (=spermathecal stalk). The duct fuses with the oviduct inside the body tegument. Canalis junctor well developed and coiled; attached to the spermatheca at the narrowest section (Fig. 2).

Penial gland with a small conical papilla. Papilla with roughened surface and blunt apex, length 5·5 mm, maximum diameter 2·7 mm. Penial gland with 18 uniform non-bifurcated tubular diverticula. These are tightly coiled and are sheathed by a thick pellicle in the proximal region (Fig. 3). Each diverticulum has a diameter of 0·5 mm and a maximum length of 6·0 mm.

Total length of penis is 16·0 mm, with a maximum diameter of 1·6 mm, consisting of a short conical stalk, only 1·5 mm 'long and a long glans which is attached to the pointed region of stalk. Base of glans slightly flattened, on one side two flaps which are somewhat folded and notched basally; while on the reverse the glans is fused with the stalk and is delimited only by a transversal rib (Fig. 15). The remaining region of the glans is cylindrical, with the distal end having a rhomboid apex and a median opening.

COMMENTS
Simroth's (1914) extensive description concentrated predominantly on structures of very little specific value and the illustrations provide little additional information. The synonymy proposed by Hoffman (1925) will be discussed in a later paper.

Vaginula fusca Heynemann

Vaginula fusca Heynemann, 1885 : 6–7, pl. 1, figs 1–3.
Cylindricaulus fuscus (Haynemann); Hoffmann, 1925 : 157, 208, 238–239, pl. 5, figs 45d, 7 (*partim*).

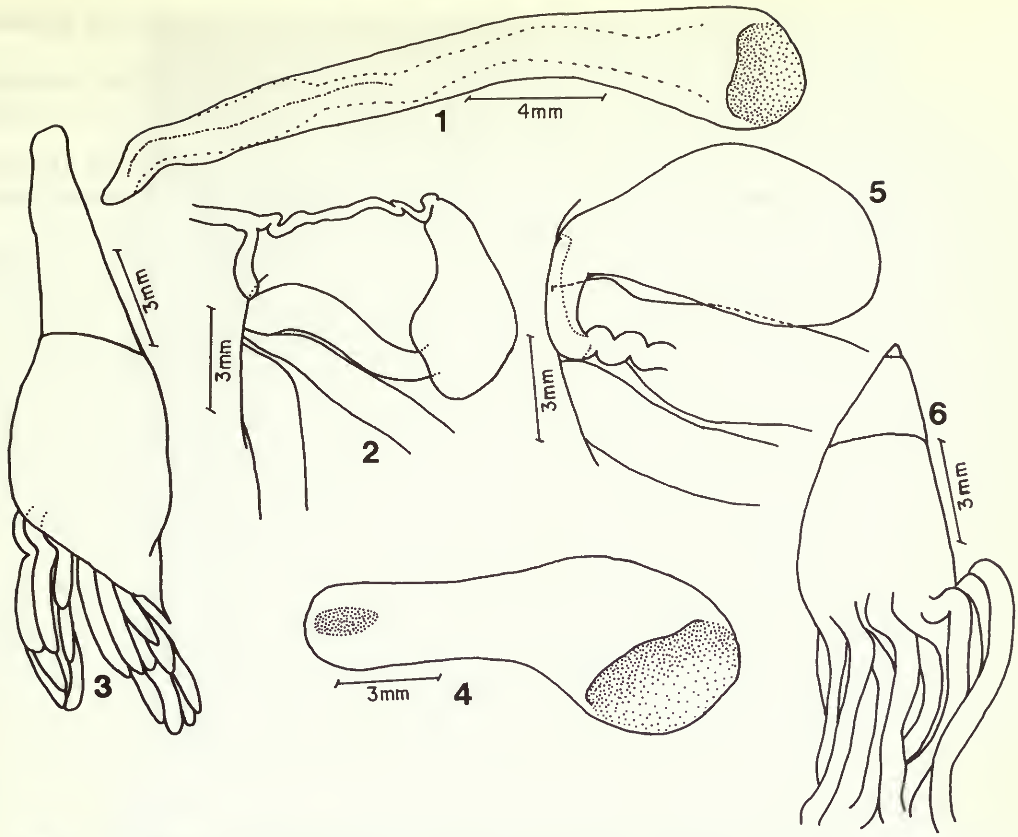
HOLOTYPE. BM(NH) Reg. No. 1896.6.5.72.

TYPE LOCALITY. Rio de Janeiro, Guanabara, Brazil.

LEG. Dr Cunningham in 1867; presented to the museum by the Lords of the Admiralty.

The specimen was well preserved both for colour and internal anatomy; previously it had not been dissected. The penis and the penial gland were removed and placed in a small tube in the jar with the specimen.

EXTERNAL MORPHOLOGY (Pl. 2, figs 1–3)
Size. Length: 81 mm; breadth: 30 mm; height: 21 mm; right hyponotum width: 12·7 mm; sole



Figs 1–3 *Vaginula cordillerae* Simroth (Holotype: BM(NH) Reg. No. 1928.8.27.26): 1. Pedal gland, dorsal view; 2. Organs close to the female genital opening, dorsal view; 3. Penial gland.

Figs 4–6 *Vaginula fusca* Heynemann (Holotype: BM(NH) Reg. No. 1896.6.5.72): 4. Pedal gland, dorsal view; 5. Organs close to the female genital opening, dorsal view; 6. Penial gland, laking distal ends of tubular glands.

width: 14·6 mm; distance of female opening from anterior end: 37 mm, from posterior end: 28·5 mm, from pedal groove: 3·2 mm.

Description. Animal large, with a slightly greater width than height; outline elliptical in dorsal view and specimen scarcely arched above ventral region. Mantle thick and hard. Notum brown with irregularly distributed black pigmentation; pigmentation a little denser on the posterior and right sides, while in the median region a thin, irregular line remains. Perinotum whitish and devoid of pigmentation, sharpened. Hyponota whitish and without pigmentation, position inclined becoming almost vertical. Sole whitish, wide and with a very distinct median line. Female opening about 1/4 distant from pedal groove and posterior to mid-point of body length. Circular anus situated to the right of sagittal plane, inside the hyponotum, but beyond the pedal groove with which it is in contact in the mid-region; closed by a well-developed opercular blade and completely covered by the posterior foot end. End of foot wrinkled and devoid of pigmentation.

INTERNAL MORPHOLOGY (Figs 4–6, 18)

Digestive system. Anterior intestinal loop covered by a lobe of the digestive gland, which is 6·5 mm wide and with the loose extremity folded forwards. Rectum penetrating body wall near to the oviduct and above it (Fig. 5).

Nervous system. The pedal nerves have separate origins and diverge for the first 15·0 mm, then proceed in parallel till the posterior region of the body cavity. Total length: 45·0 mm; maximum distance separating nerves: 11·0 mm. Pedal nerves loosely attached to the foot sole and approach close to the aorta beneath the pedal ganglion. Nerves infested with nematodes.

Pedal gland. Thin, very flattened, loose and coloured yellow. Outer zone wide, clearly delimited for the majority of its length. Length in natural position: 11·0 mm; distended: 13·0 mm; width: 2·0 mm (Fig. 4).

Reproductive system. Spermatheca pear-shaped, sessile, fusing with the oviduct inside the tegument. Canalis junctor short and thick; attached to the spermatheca at the pointed extremity close to the tegument (Fig. 5).

Penial gland with a conical papilla that is 2·1 mm long and with maximum diameter of 3·0 mm. Papilla without nipple, but showing a slight constriction at apex. Penial gland with 34 non-bifurcated or differentiated diverticula. Each diverticulum having a diameter of approximately 0·6 mm and a maximum length of between 50 and 60 mm, except for one which is 7·0 mm.

Total length of penis is 7·0 mm and a width of 2·1 mm with a maximum thickness of 0·8 mm; possessing a short conical stalk extending into a slightly flattened glans. Glans is S-shaped with well-developed lateral flaps, base marked on one surface by a transversal rib. Concave face of the first curve of the S and convex face of the second are smooth and flat. The opposite face of the first curve is at first enlarged, rapidly becoming slender and continuing through the second as a rib between the flaps. A slender and crenulate lip covers the opening at the tip of the penis.

COMMENTS

In the original description only data on external morphology were presented. Hoffmann's (1925) redescription was still insufficient for an accurate identification, and the illustration of the penis was particularly poor. The synonymy proposed by Hoffmann will be discussed in a further work. Divergence between the measurements given in the different descriptions can be attributed to variations in methods employed.

Veronicella laevis Blainville

Veronicella laevis Blainville, 1817 : 440–442, pl. 2, figs IV (1/2).
Belocaulus sloanei Hoffmann, 1925 : 249–250 (*partim*), *non* Cuvier.

HOLOTYPE. BM(NH) Reg. No. 196852-W.

TYPE LOCALITY. Unknown.

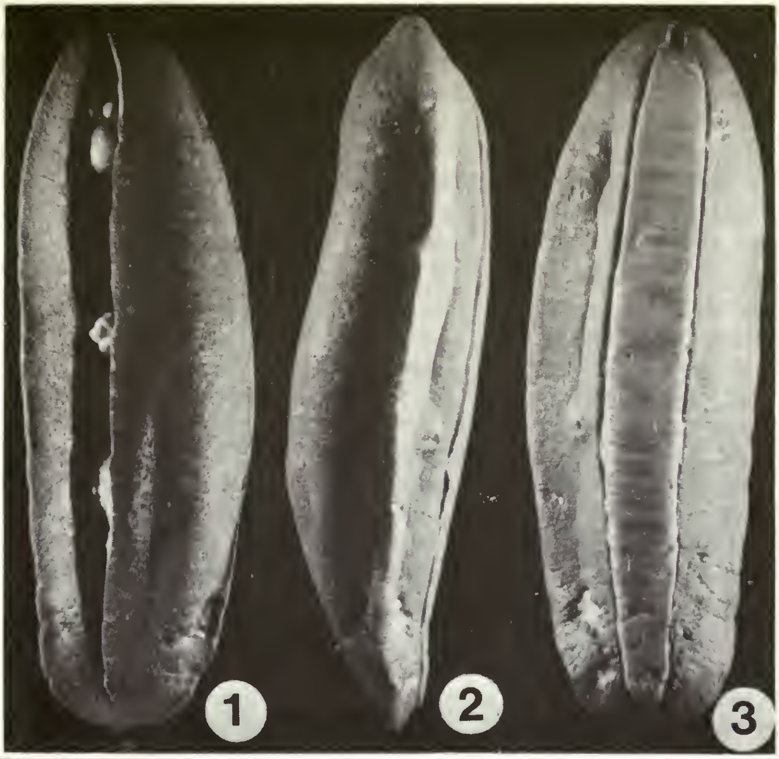
LEG. Unknown, no date.

The specimen was preserved in alcohol and discoloured. No anatomical dissection had been undertaken, in spite of an irregular longitudinal incision present in the posterior dorsal region of the notum. A piece of the very hard albumen gland had been removed and was found associated with the specimen; the remainder was found inside the specimen. There was also a short longitudinal incision in the anterior region of the notum, limited damage to the anterior sole region and a circular hole in the pedal groove, near the anus. Three labels were found inside the glass: a strip of paper written: '12. *Veronicella laevis* Blainv. Type.'; a rectangular piece of paper, written in two lines: '*Veronicella laevis* BL. – Jamaica Mus. Sloane'; a larger rectangular piece of paper, written in five lines: 'HOLOTYPE – *Veronicella laevis* Blainville 1817 – Jamaica Mus. Sloane – Sec. Journ. de Physique, LXXXV, dec. 1817, 442 – Sec. Cockerell, The Conchologist, Vol. 2, No. 8, Dec. 1893, p. 217'.

The slug was dissected with a cut along the left pedal groove. Only the penis and the penial gland were removed and these were placed in a small tube associated with the specimen. Preservation of internal organs was good.

EXTERNAL MORPHOLOGY (Pl. 1, figs 4–6)

Size. Length: 64 mm; breadth: 26 mm; height: 10·5 mm; right hyponotum width: 6·4 mm; sole width: 6·9 mm; distance of female opening from anterior end: 27·5 mm, from posterior end: 20·5 mm, from pedal groove: 2·2 mm.



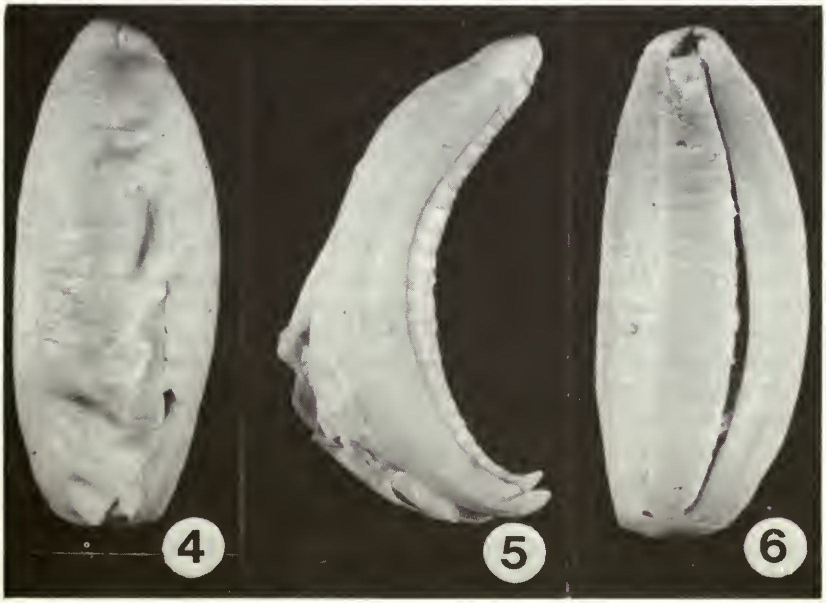


Plate 1

Figs 1–3 *Vaginula cordillerae* Simroth (Holotype: BM(NH) Reg. No. 1928.8.27.26). Dorsal, lateral and ventral view. × 1·708.

Figs 4–6 *Veronicella laevis* Blainville (Holotype: BM(NH) Reg. No. 196852-W). Dorsal, lateral and ventral view. × 1·5.

Description. Animal medium size, with a greater width than height, slightly arched dorsally, outline oblong with extremities quite pointed. Mantle thin. Notum, as well as the remaining area of the body, whitish and discoloured. Perinotum sharpened and keeled. Hyponota almost horizontal. Sole slightly more yellowish than other areas of the body and devoid of median line. Position of female opening distant about 1/3 of the hyponotum from the pedal groove and posterior to the mid-point of the body. Circular anus extends from the pedal groove into the hyponotum and to the right of the sagittal plane; partially closed by a small thin operculate blade, and partially covered by loose posterior region of the foot. The latter is not papillose or pigmented.

INTERNAL MORPHOLOGY (Figs 7–9, 17)

Digestive system. Anterior intestinal loop covered by a lobe of the digestive gland, which is 2·5 mm wide. Rectum penetrating body wall near the vagina and above it (Fig. 8).

Nervous system. Pedal nerves originate together, run parallel and unattached for 1/6 of their length until they diverge. Then adhering to the tegument extend almost parallel to the end of the body cavity where they disappear into the tegument. Total length of pedal nerves: 35·0 mm; divergent for 29·0 mm; maximum distance separating parallel nerves: 5·5 mm; meeting aorta at 2·5 mm.

Pedal gland. Small, flattened, loose and coloured yellow. External zone poorly delimited and only recognizable in the proximal region. A median concavity visible on the dorsal face at the distal region. Length: 5·2 mm; width: 1·4 mm (Fig. 7).

Reproductive system. Spermatheca subspherical, small, with a thick, rigid and very long duct. The latter fuses with the oviduct just prior to the latter joining a short vagina outside the tegument. Canalis junctor short, straight, thin, penetrating the duct at about 1/5 from the distal end, closer therefore to the spermatheca (Fig. 8).

Penial gland small, with a minute rhomboid conical papilla 0·7 mm long and 0·9 mm wide at the base. Sixteen external diverticula on the penial gland each up to 4·5 mm long and with diameter of 0·3 mm; these differ little from the 11 internal diverticula which are up to 2·5 mm long and 0·3 mm diameter. All diverticula are wrinkled and of the same colour (Fig. 9).

Total length of penis 13·5 mm with a diameter of 1·0 mm, except for a swelling at the distal end where there is an extrovertion of conical cavernous tissue, with a maximum diameter of 1·5 mm. Penis smooth, elongated and cylindrical with the deferens opening at the tip of the extrovertion (Fig. 17).

COMMENTS

This species presents a polemic problem, for Blainville (1817) in the original description, mentioned the presence of '. . . vers le tiers postérieur, un rudiment de coquille, sans aucune trace de disque ou de bouclier' (p. 442) and stated on the same page: 'On ignore tout-à-fait sa patrie, et même comment il est arrivé dans la collection', referring to material in the British Museum (Natural History) collection. On the basis of these statements, and without ever checking the type specimen, many authors have rejected the doubted validity of this species or included it in the synonymy of *V. sloanei* (Cuvier, 1817 : 411). The latter must, however, be considered as an independent species.

Blainville (1817) described the species *Veronicella laevis* and established the genus *Veronicella*, on the basis of a single specimen in the British Museum (Natural History) collection, but with no reference to its origin. Examination of the type specimen preserved in that Institution permits comparison with Blainville's drawings and description; compare plate I, figs 5 (lateral) and 6 (ventral) with plate II, drawings 1 and 2 by Blainville (1817). The conspicuous anus was interpreted by Blainville as the opening of pneumostoma and the circular hole a little ahead of the anus, which is an artifact, was thought by Blainville to be the anus, but these features together with the anterior tentacles inside the anterior edge of the mantle and the penis close to the right tentacle, all confirm Blainville's description. Finally the reference to an internal shell in Blainville, at the median posterior dorsal region and visible through the notum, can be attributed to the presence in that region of the large, but abnormally hardened, albumen gland.

Blainville (1817 : 441) comments: 'le dos est assez élevé, convexe dans les deux sens et un peu plus gibbeux ou élevé à la partie postérieure', these features are visible. There follows: 'C'est à ce point, ou environ au tiers postérieur, que l'on trouve dans l'interieur de la peau un rudiment de coquille que l'on aperçoit à travers la peau, fort mince en cet endroit', which corresponds perfectly to the rectangular, thin, still portion of the hardened albumen gland, which Blainville interpreted as an internal rudimental shell. Blainville's mistake is quite understandable if we consider that he was the first to describe a slug of this gastropod group, the only one that does not present, in any phase of its ontogeny, any trace of shell.

This redescription should remove the polemic nature of the species particularly that concerned with the validity of Blainville's species and, therefore, the priority of the taxon, which is the 'type-species' of the genus *Veronicella* Blainville, 1817. The latter being the 'type-genus' of the family Veronicellidae Gray, 1840. A more detailed taxonomic and synonymic discussion on this problem will be presented in a forthcoming paper.

Vaginula nesiotis Simroth

Vaginula nesiotis Simroth, 1914 : 297–300, pl. 12, figs 36–42.
Cylindrocaulus olivaceus var. *jamaicensis* Hoffmann, 1925 : 233–234 (*partim*), *non* Cockerell.

HOLOTYPE. BM(NH) Reg. No. 1928.8.27.28.

TYPE LOCALITY. Kingston, Jamaica.

LEG. Dr O. Fuhrmann (purch. Dr O. Fuhrmann, 1928), no date.

The specimen has been so damaged that the presence of the mantle and foot sole only permit recognition as a member of the family Veronicellidae (Pl. 2, fig. 7). All other organs have been completely macerated. Nevertheless, it is possible to verify that the specimen was opened at the notum. Thus Simroth's original, but incomplete, description is the only means for reidentification of the species. The synonymy proposed by Hoffmann (1925) is unreliable as it is based on incomplete morphological data.

Vaginula nigra Haynemann

Vaginula nigra Haynemann, 1885 : 7, pl. 1, figs 4–5.
Phyllocaulus gayi (Fischer); Hoffmann, 1925 : 244–245 (*partim*).

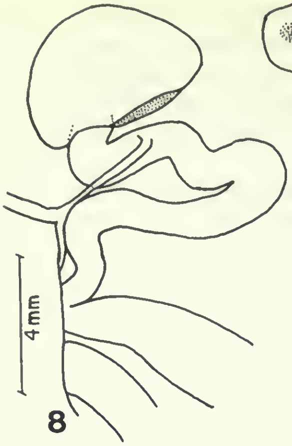
LECTOTYPE. BM(NH) Reg. No. 1876.9.30.2, selected here.

TYPE LOCALITY. Unknown, but probably Chile.

LEG. E. Gerrard Junior, no date.

Two complete specimens were present and these had not been dissected. The largest was selected as lectotype, because of its better preservation with only the penial gland abnormally soft. The paralectotype was poorly fixed; the penis was partially everted, and macerated while the other organs were also soft. Both specimens have the shiny appearance and soft consistency typical of slugs that were dying or already dead before fixation.

EXTERNAL MORPHOLOGY (Pl. 3, figs 1–3)
Size. Length: 74 mm; width: 27 mm; height: 14 mm; right hyponotum width: 7·9 mm; sole width: 7·9 mm; distance of female opening from anterior end: 26 mm, from posterior end: 36 mm, from pedal groove: 2·4 mm. (Note: dimensions of the paralectotype in the same order: 68, 27, 14, 9·9, 8·5, 25·5, 31·5 and 2·4 mm.)
Description. Animal large, with a greater width than height; outline oblong; specimen not arched, but of a soft consistency, that has contributed to the production of a cylindroid form. Colour grey, with brown staining, notum densely covered with black spots which are uniformly distributed. Perinotum not clearly defined and recognized only by a line separating the pigmented notum from the non-pigmented hyponota. The latter has a dark grey uniform colour with pale brown spots in some areas, especially near the female opening. Sole pale, without pigmentation and with a median line. Position of female opening is about 1/3 of the hyponotum from the pedal



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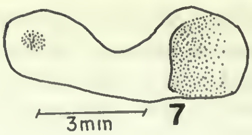

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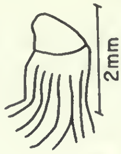

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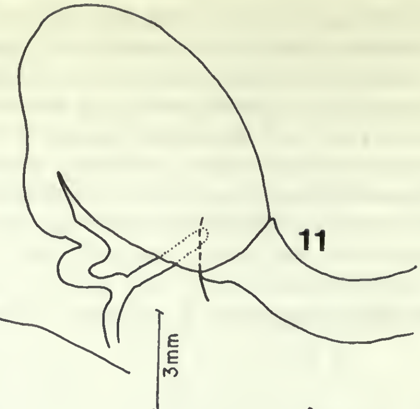

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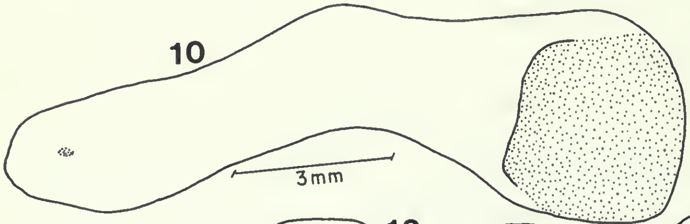

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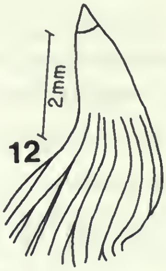

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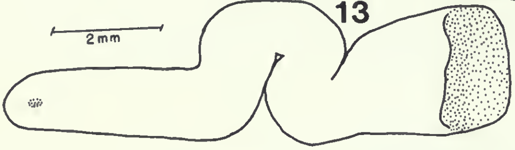

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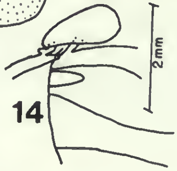

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Figs 7–9 *Veronicella laevis* Blainville (Holotype: BM(NH) Reg. No. 196852-W): 7. Pedal gland, dorsal view; 8. Organs close to the female genital opening, dorsal view; 9. Penial gland, laking distal ends of tubular glands.

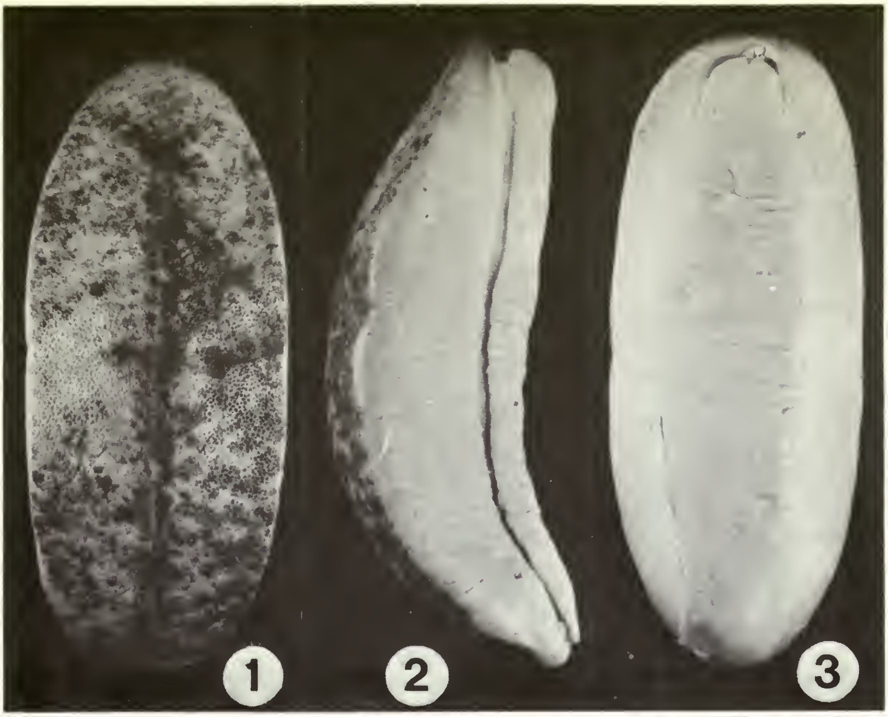
Figs 10–12 *Vaginula nigra* Haynemann (Lectotype: BM(NH) Reg. No. 1876.9.30.2): 10. Pedal gland, dorsal view; 11. Organs close to the female genital opening, dorsal view; 12. Penial gland, laking distal ends of tubular glands.

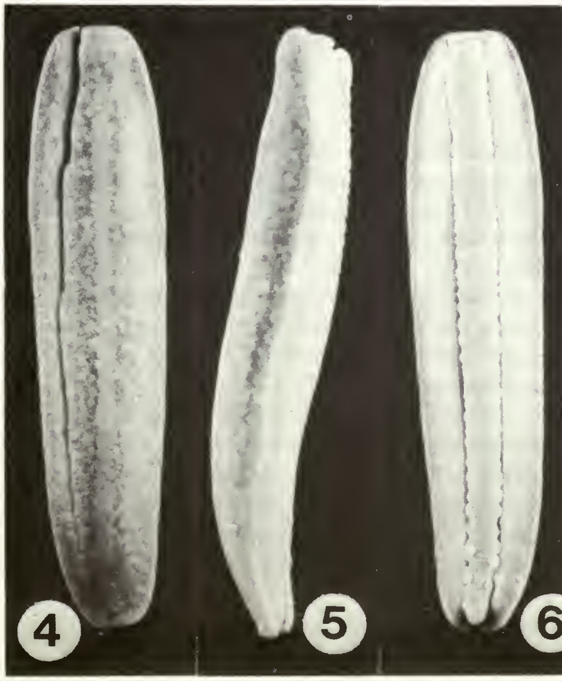
Figs 13–14 *Vaginula columbiana* Simroth (Paralectotype: BM(NH) Reg. No. 1928.8.27.27): 13. Pedal gland, dorsal view; 14. Organs close to the female genital opening, dorsal view.

groove and well anterior to mid-point of body length. Circular anus situated to the right of sagittal plane, inside the hyponotum, but in contact with the pedal groove; it is almost closed by an operculate blade and completely covered by the loose tip of the foot ending. The latter is papillous and heavily pigmented black.

INTERNAL MORPHOLOGY (Figs 10–12, 16)

Digestive system. Anterior intestinal loop covered by a lobe of the digestive gland, which is 5·0 mm wide. Rectum penetrating body wall 7·0 mm behind the oviduct and slightly above it (Fig. 11). *Nervous system.* The pedal nerves originate close together and extend parallel until meeting aorta; then diverging for 15·0 mm and becoming parallel until the posterior end of the body cavity. Nerves attached to the tegument. Total length of pedal nerves: 44·0 mm; maximum distance separating the nerves: 4·0 mm; meeting aorta at 4·5 mm.
Pedal gland. Thick, somewhat flattened, loose and coloured yellow. No external zone observed. Length in natural position: 8·5 mm; distended: 10·0 mm; width: 2·0 mm (Fig. 10).





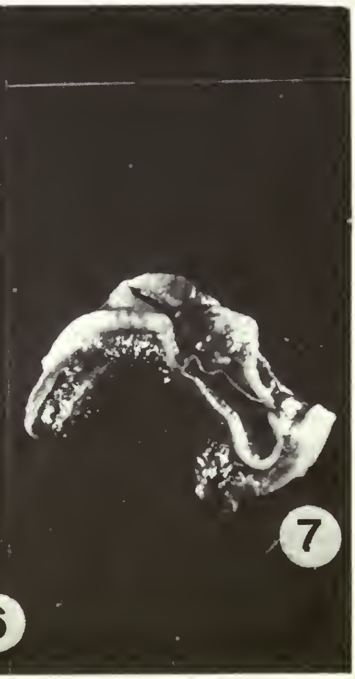


Plate 2

Figs 1–3 *Vaginula fusca* Haynemann (Holotype: BM(NH) Reg. No. 1896.6.5.72). Dorsal, lateral and ventral view. × 1·25.

Figs 4–6 *Vaginula columbiana* Simroth (Paralectotype: BM(NH) Reg. No. 1928.8.27.27). Dorsal, lateral and ventral view. × 2·06 – × 2·06 – × 2·09.

Fig. 7 *Vaginula nesiotis* Simroth (Holotype: BM(NH) Reg. No. 1928.8.27.28). View of the dried and macerated remaining portion. × 1·74.

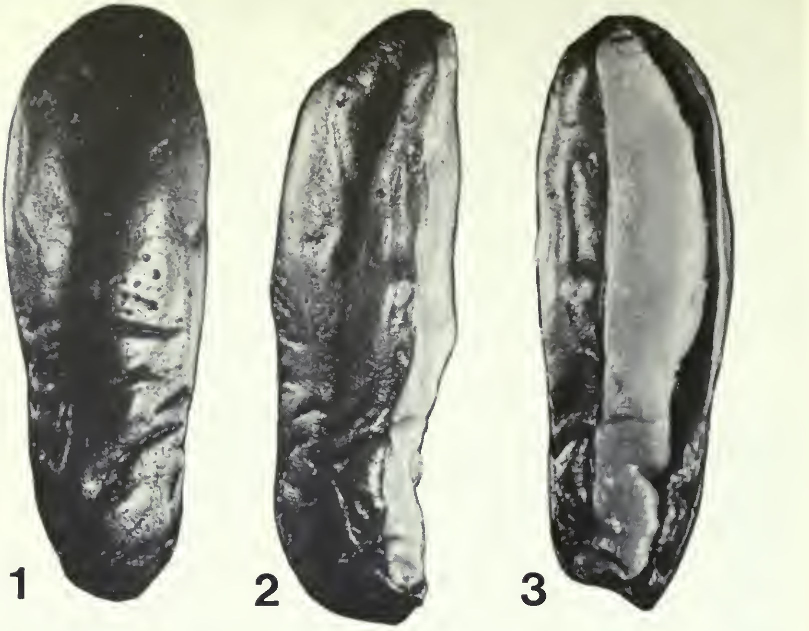


Plate 3

Figs 1–3 *Vaginula nigra* Heynemann (Lectotype: BM(NH) Reg. No. 1876.9.30.2). Dorsal, lateral and ventral view. × 1·40 – × 1·40 – × 1·35.

Reproductive system. Spermatheca egg-shaped exhibiting laterally, close to the broadest end, a small cylindrical swollen region; with fine walls, sessile, joining the oviduct inside the tegument. The thick and short canalis junctor is attached to spermatheca at the tip of the cylindrical swollen region (Fig. 11). Penial gland small, with a tiny, conicle, pointed papilla, but without nipple. Papilla 0·5 mm long and with 0·5 mm diameter at the base.

Penial gland with 17 external diverticula each up to 30·0 mm long and 0·3 mm in diameter; there are 9, light coloured, internal diverticula each up to 20·0 mm long and 0·2 mm in diameter. Distinction between the internal and external diverticula is not very sharp; no bifurcations were seen; all are very thin at the base, soft and flattened (Fig. 12).

Penis is 9·5 mm long, 3·5 mm wide and 2·3 mm thick, with a short conical stalk, from which arises a fleshy and wide spathe. The spathe is smooth with one edge being thicker than the other and showing lengthwise on the outer surface a median ridge, resembling the spine of a book. The glans is cylindrical with the distal region pointed, with the opening of the deferens at the tip; glans attached near to the base of the spathe. The spathe is longer than the glans and slightly encloses it, yet both remain separate. Spathe length: 8·0 mm and 0·8 mm thick. Length of glans: 7·0 mm, with a maximum diameter of 1·9 mm (Fig. 16).

COMMENTS

On the basis of the original description by Heynemann (1885) only the two specimens could be recognized, although the species was indeterminate. The synonymy proposed by Hoffmann (1925) will be discussed in a forthcoming paper.

Vaginula columbiana Simroth

Vaginula columbiana Simroth, 1914 : 300–303, pl. 12, figs 43–45.
Vaginula columbiana Simroth; Thomé, 1970 : 76–78, figs 8–14.

Paralectotype. BM(NH) Reg. No. 1928.8.27.27.

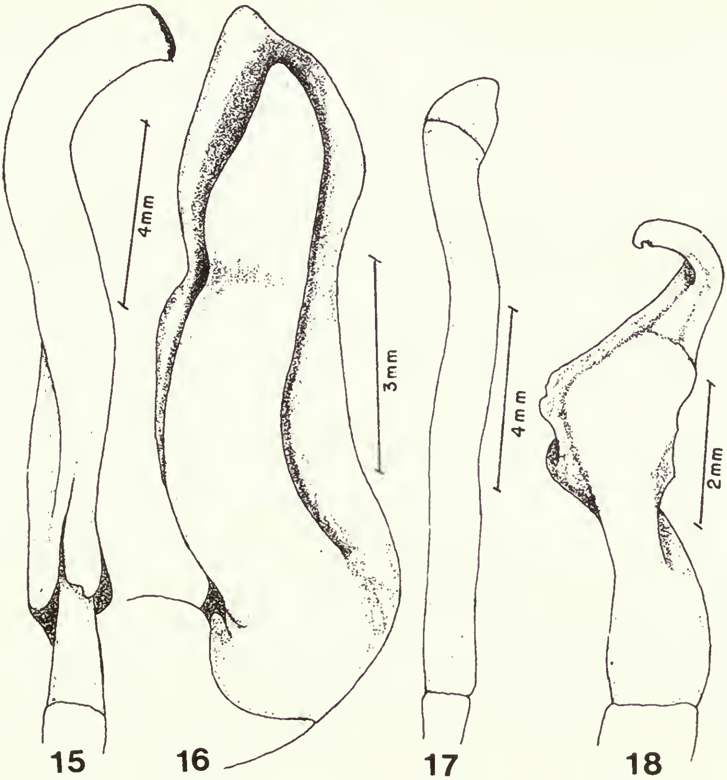
Locality. Columbia.

Leg. Dr O. Fuhrmann, no date.

The specimen was preserved in alcohol and it had previously been opened longitudinally along the notum. The penis and the penial gland were missing. The specimen was very young and immature.

External morphology (Pl. 2, figs 4–6)
Size. Length: 41 mm; width: 10·5 mm; height: 6 mm; right hyponotum width: 4·1 mm; sole width: 2·7 mm; distance of female opening from anterior end: 23 mm, from posterior end: 16 mm, from pedal groove: 1·3 mm.
Description. Shape and colour identical to that described for the Lectotype (Thomé, 1970). In this specimen there is a single outgrowth on the perinotum at the posterior end (Pl. 2, figs 4 and 6).

Internal morphology (Figs 13–14)
Digestive system. Anterior intestinal loop covered by a lobe of the digestive gland, which is 3·5 mm wide. The material was a little damaged and the typical dichotomyzation of the lobe was not observed. Rectum penetrating body wall close to and slightly above the accessory bursa, which separates it from the vagina (Fig. 14).



Penes of:

Fig. 15 *Vaginula cordillerae* Simroth (Holotype: BM(NH) Reg. No. 1928.8.27.26).

Fig. 16 *Vaginula nigra* Heynemann (Lectotype: BM(NH) Reg. No. 1876.9.30.2).

Fig. 17 *Veronicella laevis* Blainville (Holotype: BM(NH) Reg. No. 196852-W).

Fig. 18 *Vaginula fusca* Heynemann (Holotype: BM(NH) Reg. No. 1896.6.5.72).

Nervous system. The pedal nerves originate close together and run parallel almost to the end of the body cavity. They diverge very little and then only at the posterior end. They are not attached to the body wall until posterior to the point where they meet the aorta. Total length of pedal nerves: 29·0 mm; divergent for: 6·0 mm; maximum distance separating the nerves: 0·5 mm; meeting aorta at 6·0 mm.

Pedal gland. Flattened and coloured yellow. External zone light coloured and enlarged to the second fold but then indistinct. Length in natural position: 8·0 mm; distended: 10·0 mm; width: 1·3 mm (Fig. 13).

Reproductive system. Spermatheca egg-shaped, but quite pointed; attached to a cylindrical duct, and joins the oviduct posterior to the well-developed vagina which penetrates the body wall. Canalis junctor short and attaches to spermatheca near to its narrowest point. Between vagina and the rectum there is an accessory bursa, which is bell-shaped (Fig. 14).

The penial gland and the penis were not present in the specimen examined.

COMMENTS

The specimen is considered as a paralectotype because it was part of Simroth's (1914) original type species. This specimen was referred to by Simroth as being from Bogota. It is registered in the museum as being from Columbia and having been purchased from Dr O. Fuhrmann in 1928. Both the external and internal morphology permit this specimen to be specifically identified in spite of the absence of the penis and the penial gland and the sexual immaturity.

Acknowledgements

The author is indebted to John F. Peake of the Department of Zoology, British Museum (Natural History), for revision of the manuscript and also to the staff of the Mollusca Section for facilitating access to the material and bibliography as well as for kind and constant help.

I am indebted to my wife who took all the photographs and helped me with the bibliography.

The author was granted a scholarship from the 'Alexander von Humboldt-Stiftung', Bad Godesberg, Germany, which permitted a visit to London.

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Manuscript accepted for publication 8 October, 1974

A taxonomic study of six species of *Upogebia* Leach (Crustacea, Decapoda, Thalassinidea) in the collections of the British Museum (Natural History), London

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Synopsis

A recent study of unnamed specimens of *Upogebia* in the collections of the British Museum (Natural History) has enabled me to identify the following six species from among this material: *Upogebia africana* Ortmann, *Upogebia brasiliensis* Holthuis, *Upogebia carinicauda* (Stimpson), *Upogebia darwini* (Miers), *Upogebia issaeffi* (Balss) and *Upogebia spinigera* (Smith). Detailed descriptions are given here of the two species *Upogebia africana* Ortmann and *Upogebia issaeffi* (Balss) as previous accounts are inadequate for comparative studies with other species. The morphological variation of the other four species is described and discussed.

Introduction

The subgeneric division of the genus *Upogebia* into the two subgenera, *Upogebia* (*Upogebia*) Leach and *Upogebia* (*Calliadne*) Strahl, as proposed by de Man (1928) is not used in the present work. De Man assigned the species with a spine on the antero-lateral margin of the carapace, and in which the fixed finger (propodal prolongation) of the cheliped is much shorter than the dactylus to the subgenus *Upogebia*, while he placed species in which the antero-lateral carapace spine is absent and in which the cheliped fixed finger is as long as the dactylus into the subgenus *Calliadne*. Although many species of *Upogebia* can be easily assigned to one or the other subgenus on these above-mentioned features, a few show considerable variation in these respects, for example, in the present study some specimens of *Upogebia brasiliensis* and *Upogebia spinigera* cannot be satisfactorily placed in either subgenus. It has been suggested by Bozic and de Saint Laurent (1972) that before subgeneric partitioning of *Upogebia* can be reconsidered, it will be necessary to examine critically many additional characters, such as branchial formula, mouth appendages, epipods, pereiopods, etc.

The measurements given are carapace lengths (c.l.) measured from the rostral apex to the carapace posterior margin in the mid-line, and the total lengths (t.l.) measured from the rostral apex to the telson posterior margin.

Upogebia africana Ortmann

(Figs 1a–h, 2a–l)

Upogebia africana, Ortmann, 1894 : 22, pl. 2, fig. 4a, b; *Upogebia capensis* Stebbing, 1900 : 45; Stebbing, 1910 : 370; *Upogebia africana* de Man, 1928 : 37, 51; *Upogebia africana* Barnard, 1947 : 380; Barnard, 1950 : 519, 520.

Material examined. Port Elizabeth, S. Africa, 1891, 2 ♂♂, c.l. 20 mm, t.l. 57 mm; 2 ♀♀, c.l. 20 mm, 21 mm, t.l. 60 mm, 62 mm.
Port Alfred, S. Africa, 1905, 1 ♂, c.l. 23 mm, t.l. 63 mm.

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Bull. Br. Mus. nat. Hist. (Zool.) **35** (2): 127–200

Issued 26 April, 1979

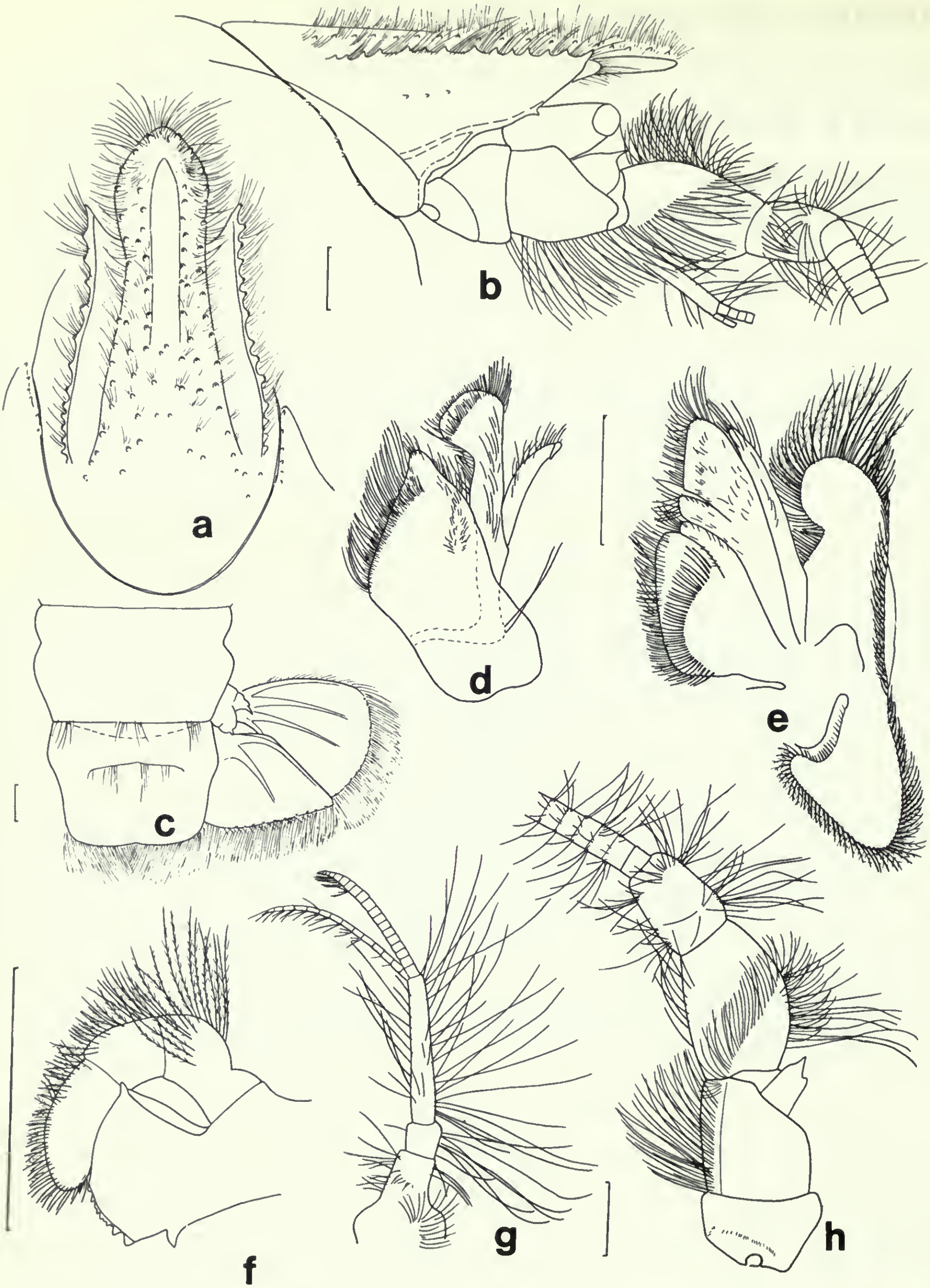

Fig. 1 *Upogebia africana* Ortmann, ♂, 63 mm t.l., Port Alfred: (a) rostrum, dorsal view; (b) rostrum, lateral view; (c) sixth abdominal segment, telson and uropods; (d) maxillule; (e) maxilla; (f) mandible; (g) antennule; (h) antenna. Scale: 2 mm.

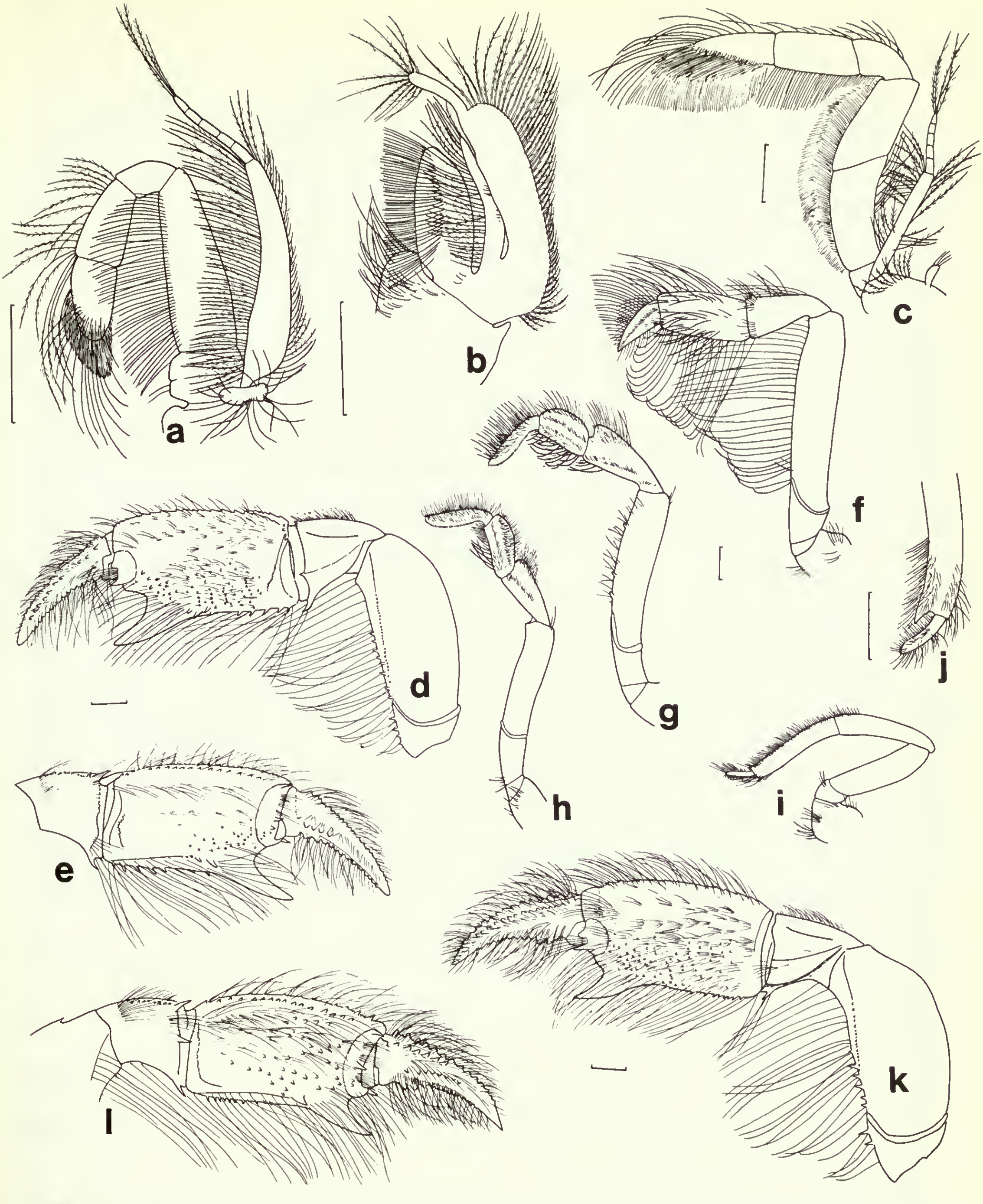

Fig. 2 (a)–(j) *Upogebia africana* Ortmann, ♂, 63 mm t.l., Port Alfred: (a) second maxilliped; (b) first maxilliped; (c) third maxilliped; (d) cheliped, outer lateral view; (e) cheliped, inner lateral view; (f) second pereiopod; (g) third pereiopod; (h) fourth pereiopod; (i) fifth pereiopod; (j) propodus and dactylus of fifth pereiopod enlarged. (k), (l) *Upogebia capensis* (Krauss), ♀, 72 mm t.l., South Africa: cheliped, outer lateral view and inner lateral view respectively. Scale: 2 mm.

DESCRIPTION. *Carapace* broad posteriorly, narrowing anteriorly. Front tridentate (Fig. 1a, b). Rostrum long and conical, setose, projecting far beyond eyes, lower margin unarmed, lateral margins each with five or six acute teeth. Lateral ridges of gastric region with 11–14 teeth, lateral grooves large and divergent posteriorly, a smooth, non-setose medio-dorsal groove anteriorly. Anterior part of gastric region between gastric ridges spinose and setose, posterior quarter unarmed and glabrous. *Linea thalassinica* distinct. Cervical groove deep, lateral part of cervical groove below *linea thalassinica* provided with small denticles in two ♂♂ out of the five specimens.
Telson (Fig. 1c) broader than long, lateral margins slightly convergent distally, postero-lateral angles rounded, posterior margin straight, median groove distinct, median and lateral carinae present but not conspicuous.
Antennule (Fig. 1g) first peduncular segment unarmed, second segment shortest, third segment slender, longer than first and second segments together, flagella simple.
Antenna (Fig. 1h) scaphocerite terminating in a spine, flagellum long and simple.
Mandible (Fig. 1f) with an inner lateral tooth, small teeth on cutting edge and a larger one basally.
Maxillule (Fig. 1d), *maxilla* (Fig. 1e) with normal shape as usually observed in *Upogebia*.
First maxilliped (Fig. 2b), *second maxilliped* (Fig. 2a) and *third maxilliped* (Fig. 2c) each with a small epipod.
Cheliped (Fig. 2d, e) slightly stouter in the male than in the female. Coxa unarmed. Ischium with 1–3 spines on lower margin. Merus with upper margin convex, with two rows of denticles on inner and outer lower margins and 5–7 large teeth proximally. Carpus with one acute spine on distal upper margin followed by a row of 5–7 denticles and another spine on lower margin; outer surface with a longitudinal groove and a smooth ridge ending in a spine, inner surface with 2–3 small denticles on distal margin between the upper and lower spines. Palm with two spinose ridges on upper margin, lower margin of outer surface spinulose proximally, with 1–4 larger spines near the base of fixed finger and another large spine near the base of dactylus; inner surface of palm spinulose distally with one or two spines near the base of fixed finger and two additional spines near the base of dactylus; fixed finger with two denticles on cutting edge in one female specimen, smooth in others. Dactylus with two spinose ridges on upper margin, cutting edge denticulate with two larger teeth near the base, inner surface with a row of 4–5 granules above cutting edge. In the female, the palm and dactylus of cheliped are less spinose than in the male. Only one spinose ridge is conspicuous on upper margin of the palm, spines and spinules are fewer and smaller on both palm and dactylus.
Second pereiopod (Fig. 2f) setose, carpus with a spine on both upper and lower distal margins, other segments unarmed.
Third pereiopod (Fig. 2g) merus with 2–4 spines on lower margin; dactylus elongated, slender, lower margin finely pectinate.
Fourth pereiopod (Fig. 2h) all segments unarmed, dactylus slender with lower margin pectinate.
Fifth pereiopod (Fig. 2i) slender, unarmed and subcheliform; propodus setose with a very small ventro-dorsal process; dactylus small, lower margin pectinate.
Pleopod 1 of the female slender, two-segmented.
Pleopods 2–5 large in both sexes; endopod ovate, exopod larger, elliptical with two blunt carinae on dorsal surface.
Uropod (Fig. 1c) broad, as long as telson; protopod with a spine near the base of endopod; endopod triangular with two longitudinal carinae, exopod rounded with three carinae and a spine on the basal part, posterior margins of both endopod and exopod nearly straight, with many minute spinules.

REMARKS. Balss (1913) and de Man (1927, 1928) considered *U. africana* Ortmann and *U. capensis* (Krauss) as identical species, but Barnard (1950) stated that the two forms appeared to be localized one in the colder water, the other in the warmer water and should be kept separate.

The present specimens have been compared with some material identified as *U. capensis* and deposited in the collections of the British Museum (Natural History). These include 2 ♂♂ from the Natal Coast, 13 mm, 14 mm c.l. and 38 mm, 40 mm t.l. and 1 ♀ from offshore South Africa, 25 mm c.l., 72 mm t.l. The similarities and differences observed are listed in Table 1.

Table 1 Comparison of *U. africana* from Port Alfred and Port Elizabeth with *U. capensis* from Natal Coast and South Africa

		U. africana	*U. capensis*	
		From Port Alfred and Port Elizabeth	From Natal Coast	From S Africa
Denticles on hind margin of cervical groove		present in 2 out of 5 specimens	present, small	present, spiniform
Cheliped	Coxal spine	absent	absent	present, large
	Spine on upper margin of merus	absent	present	present
	Large spines on lower outer margin of palm (near fixed finger)	present, 1–4	present, 1	absent
Second pereiopod	Coxal spine	absent	absent	present
	Spine on upper margin of merus	absent	absent	present

The decisive diagnostic character separating the two species (Barnard, 1950) is the presence of coxal spines on legs 1–3 in *U. capensis* and their absence in *U. africana*. In this respect, the material from Natal Coast must be reidentified as *U. africana* while the specimen from South Africa is a true *U. capensis*. Its cheliped is illustrated in Fig. 2k, l.

In addition to the absence of coxal spines on legs 1–3, the material of *U. africana* from Natal Coast and that from Port Alfred and Port Elizabeth all have 1–4 large spines on the lower outer margin of the palm of the cheliped, near the fixed finger and all without a spine on the upper distal margin of the merus of the second pereiopod.

The material of *U. africana* from Port Alfred and Port Elizabeth has no spine on the upper distal margin of the merus of the cheliped, but this spine is present in the specimens of *U. africana* from Natal Coast as well as in that of *U. capensis* from South Africa. It would appear that this variable feature cannot be used in separating the two forms.*

DISTRIBUTION. Port Elizabeth (Ortmann, 1894); Zwartkops River estuary, Algoa Bay (Stebbing, 1900); Gordon's Bay, east side of False Bay (Stebbing, 1910); Somerset Strand and Gordon's Bay, estuary of Breede River (Port Beaufort), Knysna lagoon, Keurbooms river estuary (Plettenberg Bay), Zwartkops estuary, Nahoon river estuary (East London), Port St Johns and Durban Bay (Barnard, 1950); Natal Coast, Port Alfred.

Upogebia brasiliensis Holthuis

(Fig. 3a, b)

Upogebia brasiliensis Holthuis, 1956: 175–181, figs 1, 2; *Upogebia brasiliensis* Gomes Correa, 1968: 97–109.

MATERIAL EXAMINED. Georgetown, British Guiana, 1917, 2 ♂♂, c.l. 7 mm, t.l. 21 mm, 22 mm; 3 ♀♀, c.l. 6–8 mm, t.l. 19–24 mm.

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* After the completion of this paper the author had the opportunity to examine some material of *U. capensis* from S.W. Africa (Zool. Mus. Berlin 16130) which was on loan by the Berlin Museum to Dr K. Sakai. The material included 55 specimens of 16–70 mm t.l. in which the following features were observed:

1. The antenna, both peduncle and flagellum, is more slender than that of *U. africana*.
2. Coxal spines are present on 1st–3rd pereiopods in all specimens, that of 3rd pereiopod usually small.
3. Outer surface of cheliped palm with small spinules only but without any large spines.
4. Merus of 2nd pereiopod with one spine on upper distal margin, except in two specimens.

The above observations confirm Barnard's view of separating *U. africana* and *U. capensis*.

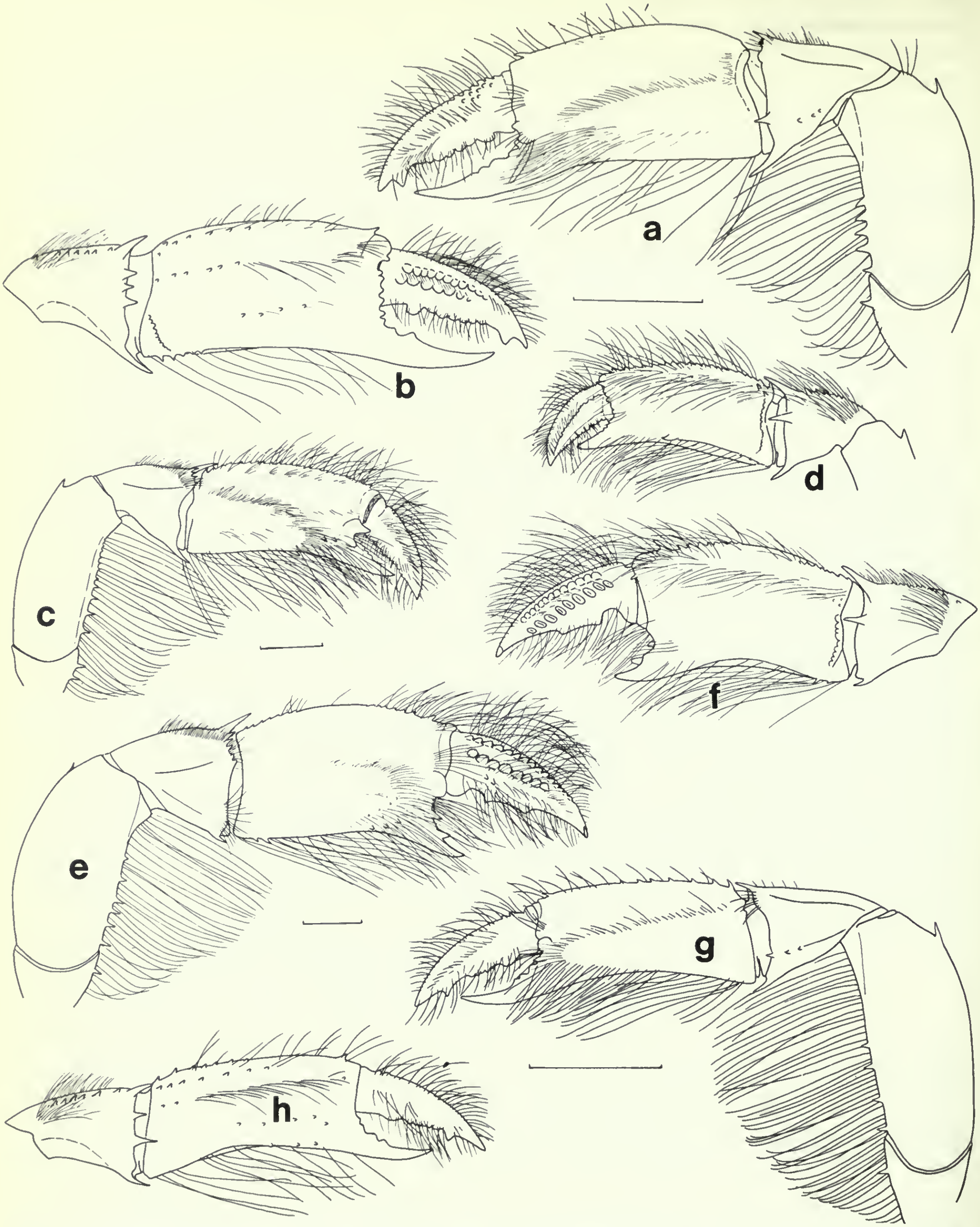

Fig. 3 Cheliped, outer lateral view and inner lateral view respectively: (a), (b) *Upogebia brasiliensis* Holthuis, ♂, 22 mm t.l., Georgetown; (c), (d) *Upogebia carinicauda* (Stimpson), ♀, 39 mm, t.l., Gulf of Siam; (e), (f) *Upogebia issaeffi* (Balss), ♀, 41 mm t.l., Tsur Island; (g), (h) *Upogebia spinigera* (Smith), ♀, 26 mm t.l., West Coast of Central America. Scale: 2 mm.

REMARKS. All specimens agree with the description of the species and with one of the type specimens examined (ovigerous ♀, 29 mm t.l.) except in the following features:

1. The spine on the antero-lateral margin of the carapace is absent in the female from Ecuador.
2. The large subterminal tooth on the cutting edge of the cheliped dactylus is absent in the three females from Georgetown.
3. The cheliped carpus of the male bears a row of six small denticles on its dorsal side, behind the anterior dorsal spine, and on the outer side, another large spine on its anterior margin, between the dorsal and ventral ones.
4. Spines on the lower margin of the cheliped merus are very small in the female from Ecuador.
5. The lower margin of the merus of the third pereiopod is unarmed in one female specimen from Georgetown.

DISTRIBUTION. Brazil (Holthuis, 1956; Gomes Correa, 1968); Georgetown, British Guiana; Esmeraldas, Ecuador.

Upogebia carinicauda (Stimpson)

(Fig. 3c, d)

Gebia carinicauda Stimpson, 1860 : 23; *Gebia barbata* Strahl, 1861 : 1062, figs 7–9; *Gebia carinicauda* Miers, 1884 : 280; *Gebia carinicauda* de Man, 1888 : 256; *Gebia barbata* Ortmann, 1892 : 54, fig. 8; *Gebia barbata* Ortmann, 1894 : 22; *Upogebia* (*Upogebia*) *carinicauda* de Man, 1926 : 341–345; de Man, 1928 : 60–65, figs 6, 6a–n; *Upogebia* (*Upogebia*) *kempi* Shenoy, 1967 : 777–804, figs 1–12; *Upogebia* (*Upogebia*) *kempi* Sankolli, 1972 : 671–682, figs 9, 10.

MATERIAL EXAMINED. Gulf of Siam, 1898, 1 ♀, c.l. 13 mm, t.l. 39 mm.

REMARKS. The present specimen is compared with material of *U. carinicauda* in the BM(NH) with three specimens of *U. carinicauda* of the Siboga Expedition and with two paratype specimens of *U. kempi* Shenoy from Bombay.

Material of *U. carinicauda*

1. Thursday Island, ♀ (BM(NH) Reg. No. 81–31) c.l. 7 mm, t.l. 20 mm
2. Thursday Island, ♂ (BM(NH) Reg. No. 82–7) c.l. 10 mm, t.l. 30 mm
3. Thursday Island, ♀ (BM(NH) Reg. No. 82–7) c.l. 12 mm, t.l. 35 mm
4. Island of Torres Straits, ♀ (BM(NH) Reg. No. 77–12) c.l. 11 mm, t.l. 33 mm
5. Ambon, Siboga Exped. St. 181, ♀, c.l. 6 mm, t.l. 21 mm
6. Ambon, Siboga Exped. St. 181, ♂, c.l. 7 mm, t.l. 23 mm
7. Ambon, Siboga Exped. St. 181, ♀, c.l. 10 mm, t.l. 32 mm

Material of *U. kempi*, two paratypes

8. Bombay, ♀, c.l. 14 mm, t.l. 45 mm
9. Bombay, ovigerous ♀, c.l. 14 mm, t.l. 46 mm

Table 2 lists the main similarities and differences observed.

The present material from the Gulf of Siam agrees very well with specimens of *U. carinicauda* identified by Miers (1884) and also with two specimens of the material from Ambon and is identical to the type specimens of *U. kempi*. With the exception of the female specimen from Ambon of 21 mm t.l., all specimens considered in Table 2 are similar in having: (*a*) four spines on the rostrum; (*b*) an antero-lateral carapace spine; (*c*) a spine on the upper distal margin of the cheliped merus; (*d*) three large spines on the inner anterior margin of the cheliped carpus; (*e*) a large spine on the lower margin of the palm near the fixed finger; and (*f*) a spine on the upper distal margin of the merus of the second pereiopod. The following variations are observed:

1. The rostrum is short in most specimens of total length less than 33 mm. In larger specimens of *U. carinicauda* and *U. kempi*, the rostrum reaches well beyond the eye-stalks.
2. The ovigerous paratype of *U. kempi* has a fairly large tubercle on the antero-lateral margin of the carapace, near the base of the antenna whilst in the other female, a few very small tubercles are present. They are absent in all specimens of *U. carinicauda*.

Table 2 Specimens of *U. carinicauda* and *U. kempi* compared, from various Indo-Pacific localities

	U. carinicauda								*U. kempi*	
	Thursday Isl.	Ambon	Ambon	Thursday Isl.	Ambon	Torres Straits	Thursday Isl.	Gulf of Siam	Bombay	Bombay
Specimen number used in text	1	5	6	2	7	4	3		8	9
Total length (mm)	20	21	23	30	32	33	35	39	45	46
Length of rostrum	about 1·5 times of eye-peduncle			about twice that of eye-peduncle	about 1·5 times that of eye-peduncle		about twice that of eye-peduncle			
Spines on rostrum	4	4	4	4	4	4	4	4	4	4
Antero-lateral carapace spine	present	absent	present	present	present	present	present	present	present	present
Tubercles on margin of carapace, near antenna	absent	absent	absent	absent	absent	absent	absent	absent	2–3, very small	1, large
Cheliped										
Spines on ischium	1	absent	1	2	absent	2	2	2	2	2
Merus: Spines on upper distal margin	1	absent	1	1	1	1	1	1	1	1
Merus: Spines on lower margin	6	absent	6	20	8	8	10	14	14	18
Carpus: Large spines on inner ant. margin	3	absent	3	3	3	3	3	3	3	3
Carpus: Denticles behind dorsal spine	4, very small	absent	absent	5	absent	4	5	6	6	5
Propodus: Row of denticles on upper margin	absent	absent	absent	distal half present	absent	present, spines larger distally	present, spines larger distally	present, spines slightly larger distally	present, spines of the same size	present, spines of the same size
Propodus: Large spine near fixed finger	present	absent	present	present	present	present	present	present	present	present
Propodus: Teeth on fixed finger	4–5	4	3	4	4	6	5	6	5	5
Second pereiopod										
Spine on upper distal margin of merus	present	absent	present	present	present	present	present	present	present	present
Third pereiopod										
Tubercles on lower margin of merus	absent	absent	absent	11–12	absent	6–7	3rd pereiopod missing	3–4	9–10	3rd pereiopod missing

3. Denticles behind the dorsal spine of the cheliped carpus are absent in all specimens from Ambon. In others, they show variation in size which seems to be related to the size of the animals.

4. Denticles on the upper margin of the cheliped palm are absent in one specimen of *U. carinicauda* from Thursday Island and in all specimens from Ambon. When they are present, it would seem that these denticles appear first on the distal part of the palm and then on the proximal part as the animals mature. They are large and apparent in the specimen from the Gulf of Siam and in the paratypes of *U. kempi*.

5. In small specimens, the telson is wider proximally than distally. In larger specimens, it approximates a rectangular shape.

6. Although having four spines on the rostrum, the female specimen from Ambon of 21 mm t.l. is devoid of nearly all other specific characters of *U. carinicauda* and the fixed finger of its cheliped is as long as the dactylus. It is probably an immature specimen, nevertheless its identification as *U. carinicauda* seems to be very uncertain.

DISTRIBUTION. Hongkong (Stimpson, 1860). Luzon (Strahl, 1861). Thursday Island, Torres Straits (Miers, 1884). Elphinstone Island, Mergui Archipelago (de Man, 1888), Samoa Island (Ortmann, 1892). Amboina (Ortmann, 1894; de Man, 1928). Buka, Salomon Islands (de Man, 1926). Anchorage of Labuan Pandan, Lombok; Anchorage off Seba, Savu; Haingsisi, Samau Island, Timor; Taruna-bay, Great-Sangir Island; Dammer; Saleyer-anchorage (de Man, 1928). Bombay, India (Shenoy, 1967; Sankolli, 1972). Gulf of Siam.

Upogebia darwini (Miers)

Gebiopsis Darwinii Miers, 1884 : 281, pl. 32, fig. A; *Gebiopsis intermedia* de Man, 1888 : 256, pl. 16, figs 6–8; *Gebiopsis Darwinii* Henderson, 1893 : 432; *Gebia* (*Gebiopsis*) *intermedia* Ortmann, 1894 : 23; *Gebiopsis intermedia* Zehntner, 1894 : 194; *Gebiopsis intermedia* Lanchester, 1901 : 555; *Upogebia intermedia* Pearson, 1905 : 91; *Upogebia* (*Calliadne*) *Darwinii* Nobili, 1906 : 97; *Upogebia* (*Calliadne*) *Darwinii* Borradaile, 1910: 262; *Upogebia* (*Calliadne*) *Darwinii* de Man, 1928 : 24, 50, 84–86, figs 12, 12a–f; *Upogebia darwini* Ngoc-Ho, 1977 : 439–464, figs 1–13.

MATERIAL EXAMINED. Singapore, 1899, 1 ♂, c.l. 12 mm, t.l. 34 mm; 2 ovigerous ♀♀, c.l. 11 mm and 11·5 mm, t.l. 31 mm and 34 mm.

REMARKS. The present material agrees with the types of the species with which it has been compared except for some variations in the spinulation of the merus cheliped lower margin. Similarly to the types, the smaller female has 9–10 spines on the merus cheliped lower margin, whilst the male has 19–20 spines and the larger female has up to 28–30 spines on this margin. In the male, those spines are large proximally and decrease in size distally; in both females, they are small.

DISTRIBUTION. Port Darwin (Miers, 1884); Singapore (Miers, 1884, present paper); Elphinstone Island, Mergui Archipelago (de Man, 1888); Rameswaram, Tutticorin, Cheval Par (Henderson, 1893); Amboina (Ortmann 1894, Zehntner 1894, de Man 1928); Pulu Bidan, Penang (Lanchester, 1901); South of Adam's Bridge and Muttuvaratu Paar (Pearson, 1905); Aden, Perim, Obock (Nobili, 1906); Saya de Malha Bank (Borradaile, 1910); Phuket, Thailand (Ngoc-Ho, 1977).

Upogebia issaeffi (Balss)

(Fig. 3e, f; Fig. 4a–i; Fig. 5a–h)

Gebia (*Upogebia*) *issaeffi* Balss, 1913 : 239; Balss, 1914 : 89–90, figs 48–49; *Upogebia* (*Upogebia*) *Issaeffi* de Man 1927 : 27–29; de Man 1928 : 39, 41; *Upogebia issaeffi* Makarov, 1938 : 59–61, figs 19, 20; *Upogebia Issaeffi* Yokoya, 1939 : 278; non *Upogebia* (*Upogebia*) *issaeffi* Sakai, 1968 : 47, fig. 1D.

MATERIAL EXAMINED. Tsur Island (Tsuru Shima or Tsuri Shima, Japan ?), 1892, 7 ♂♂, c.l. 11·5–19·5 mm, t.l. 36–58 mm; 3 ♀♀, c.l. 12–19 mm, t.l. 37–60 mm.

DESCRIPTION. Carapace broad posteriorly, narrowing anteriorly.

Front tridentate. Rostrum (Fig. 4a, b) triangular, setose, projecting far beyond eyes, lower margin unarmed, lateral margins each with four or five acute teeth. Lateral ridges of gastric region with 10–11 teeth, lateral grooves large and slightly divergent posteriorly. Anterior part of gastric region between gastric ridges spinose and setose; middle line and about 1/5 of posterior part of gastric region unarmed and glabrous. *Linea thalassinica* distinct. Cervical groove deep, lateral part below *linea thalassinica* with a few small spinules. Spine on antero-lateral margin of carapace distinct, it is bifid in two specimens.

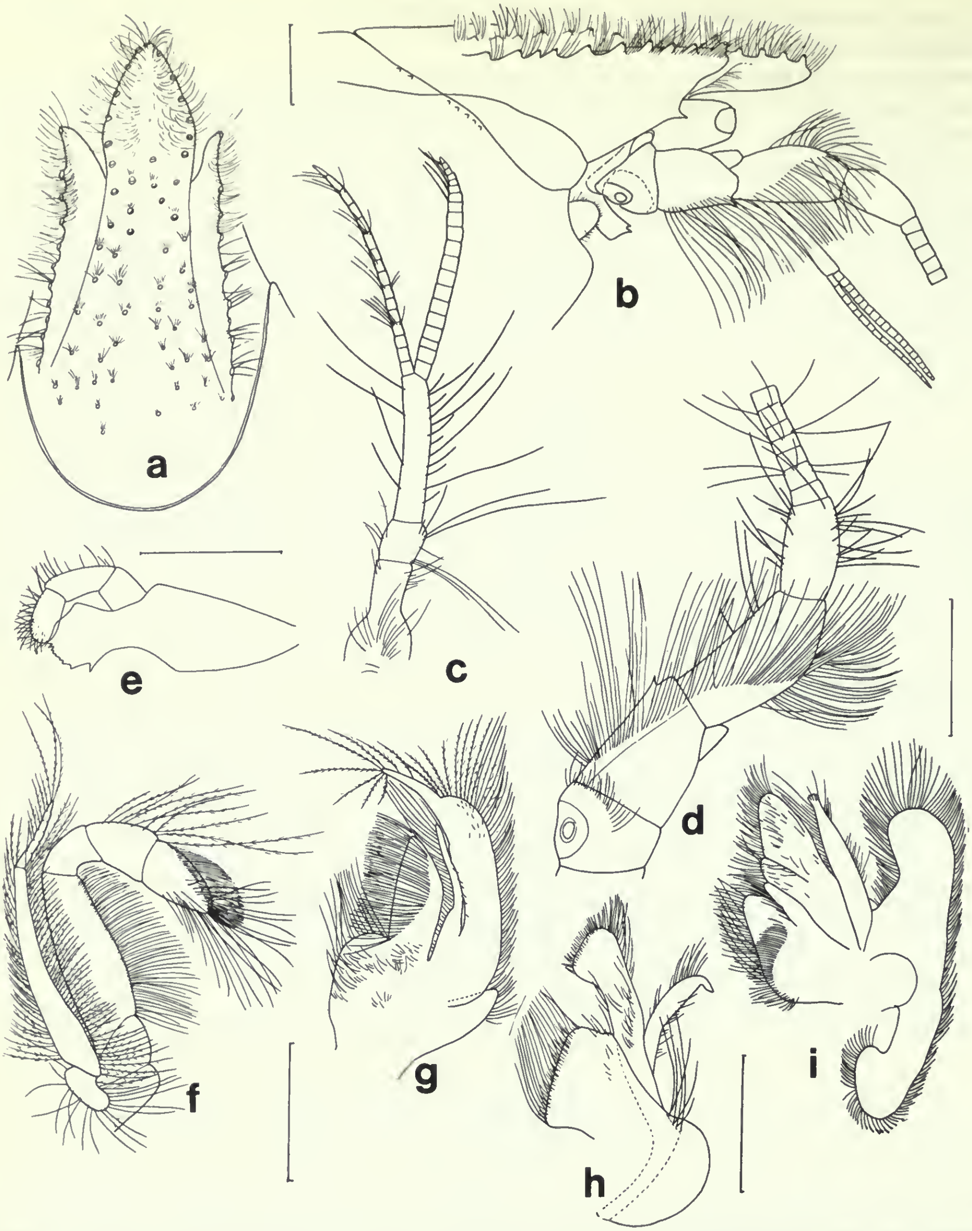

Fig. 4 *Upogebia issaeffi* (Balss), ♂, 51 mm t.l., Tsur Island: (a) rostrum, dorsal view; (b) rostrum, lateral view; (c) antennule; (d) antenna; (e) mandible; (f) second maxilliped; (g) first maxilliped; (h) maxillule; (i) maxilla. Scale: 2 mm.

Telson (Fig. 5h) about as long as sixth abdominal segment and slightly broader than long. Lateral margins a little convergent, postero-lateral angles rounded, posterior margin straight or slightly concave in the middle, median groove distinct but median and lateral carinae inconspicuous.

Antennule (Fig. 4c) first and second peduncular segments of equal length, third segment longer than first and second segments together. Flagella simple.

Antenna (Fig. 4d) second peduncular segment with a spine near distal end of lower margin, scaphocerite rounded without spine, flagellum long.

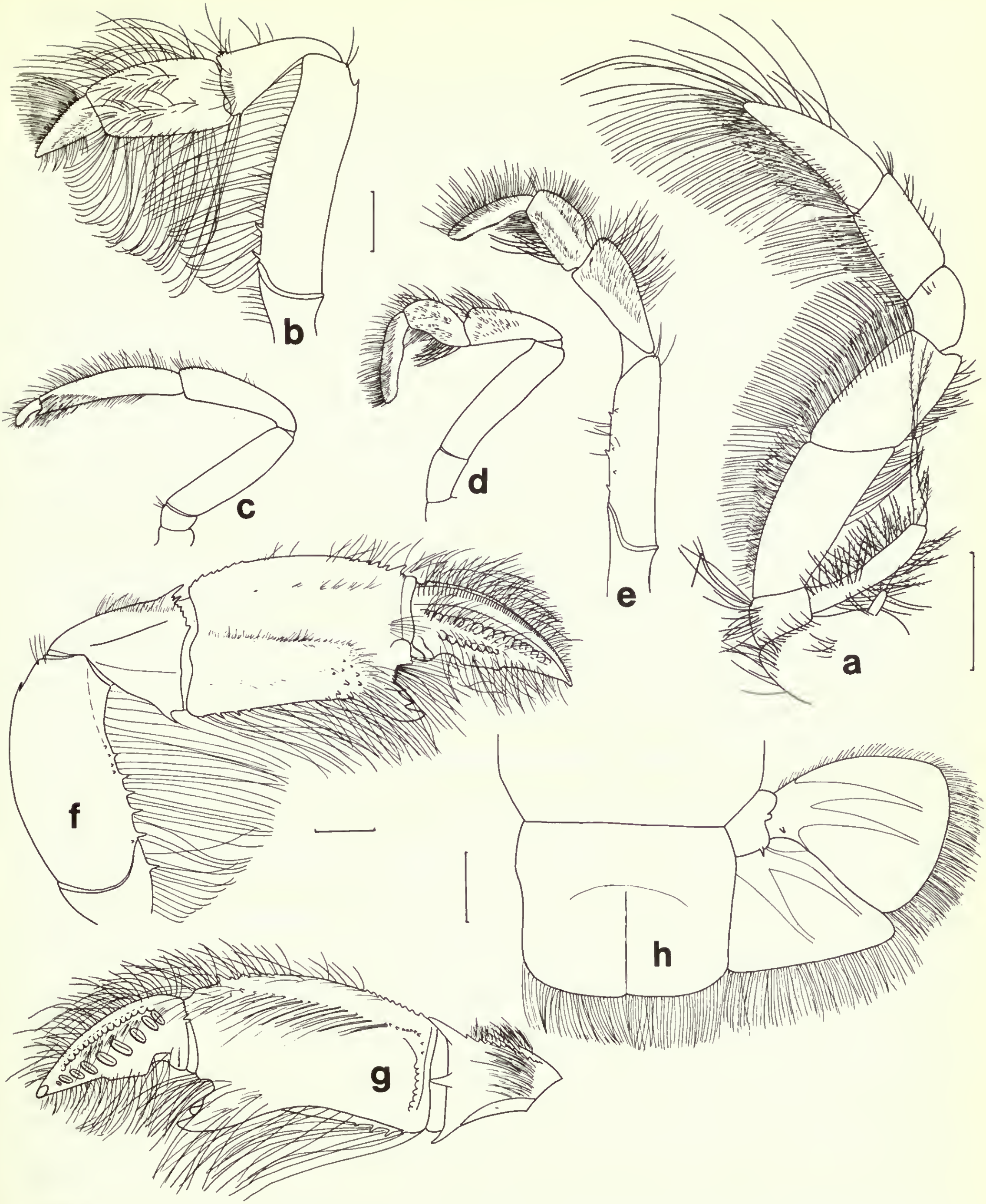

Fig. 5 *Upogebia issaeffi* (Balss), ♂, 51 mm t.l., Tsur Island: (a) third maxilliped; (b) second pereiopod; (e) third pereiopod; (d) fourth pereiopod; (c) fifth pereiopod; (f) cheliped, outer lateral view; (g) cheliped, inner lateral view; (h) telson and uropods. Scale: 2 mm.

Mandible (Fig. 4e) with small teeth on cutting edge and a larger one basally.

Maxillule (Fig. 4h), *maxilla* (Fig. 4i) apparently showing no differences with those of other *Upogebia* species.

First maxilliped (Fig. 4g) with a fairly large and rounded epipod.

Second maxilliped (Fig. 4f), *third maxilliped* (Fig. 5a) each with a small epipod.

Cheliped (Fig. 3e, f; Fig. 5f, g). Ischium with one spine near distal end of lower margin. Merus with one spine near distal end of upper margin, lower margin with a few small tubercles distally and 3–6 acute spines proximally. Upper margin of carpus with a row of 9–10 small tubercles and a large spine at distal end, on the outside of which 2–5 other small spines are present; a spine near distal end of lower margin of carpus and on the inner side, a third spine on distal margin, about halfway between the upper and the lower ones. Upper margin of propodus with a longitudinal ridge provided with small tubercles proximally and distally with 5–7 larger spines, the distal one large and acute; lower margin with two or three blunt spines proximally, with a large, sharp spine and a few tubercles near the base of fixed finger and another rounded spine near the base of dactylus; fixed finger with a large conical tooth. Dactylus setose, upper margin, in male (Fig. 5f, g), with a longitudinal crest bearing on its outer side a row of fine transverse striae; two longitudinal rows of granules on the outer side of dactylus, a row of granules and another row of oblique ridges on the inner side; cutting edge with two obtuse teeth more or less fused together. Dactylus of cheliped of female (Fig. 3e, f) without row of transverse striae on upper margin but with a row of rounded granules; two additional similar rows of granules present, one on the outer side, the other on inner side of dactylus; oblique ridges also present on inner side but much less conspicuous than in the male.

Second pereiopod (Fig. 5b). Merus with one spine near distal end of upper margin and two spines proximally on lower margin; carpus with one spine on distal end of both upper and lower margin; propodus and dactylus very setose but unarmed.

Third pereiopod (Fig. 5e). Merus with three acute teeth and a few small tubercles on lower margin; carpus and propodus setose, flattened and unarmed; dactylus slender, lower margin finely pectinate.

Fourth pereiopod (Fig. 5d). All segments unarmed, carpus and propodus very setose, lower margin of dactylus finely pectinate.

Fifth pereiopod (Fig. 5c). Propodus slender and setose with a small ventro-distal process; dactylus short.

First pleopod, in female, with two elongated segments.

Second to fifth pleopods large in both sexes; endopod rounded, exopod larger, elliptical.

Uropod (Fig. 5h) broad, as long as telson; protopod with a small spine on inner side; endopod triangular, exopod ovate, each with two longitudinal carinae.

Remarks. Balss (1913) and de Man (1927) considered the stridulating ridge on the dactylus of the cheliped an important feature for separating *U. issaeffi* from other species. However, both authors had probably examined male specimens in which this ridge is clearly present.

Makarov (1938) studying material from Vladivostok observed a sexual difference in the presence or absence of a stridulating ridge on the dactylus of the cheliped, but Sakai (1968) found no such difference in his material of *U. issaeffi* from Japan. Sakai later considered the identification of his material as incorrect (personal communication).

The present material confirms Makarov's view, the stridulating ridge is here present only in the male. As it is absent in the female, this feature can no longer be used as a distinguishing character of the species.

Distribution. Vladivostok (Balss, 1913; Makarov, 1938); Onagawa, Miyagi Pref. (Yokoya, 1939); Tsur Island.

Upogebia spinigera (Smith)

(Fig. 3g, h)

Gebia spinigera Smith, 1871 : 92–93; *Gebia longipollex* Streets, 1871 : 242; *Gebia longipollex* Lockington, 1877 : 108; Lockington, 1878 : 300; *Gebia spinigera* Lockington, 1878 : 300; *Gebia spinigera* Pocock, 1890 : 515; *Upogebia* (*Upogebia*) *longipollex* Borradaile, 1903 : 543; *Upogebia* (*Upogebia*) *spinigera* Borradaile, 1903 : 543; *Upogebia* (*Upogebia*) *longipollex* de Man, 1928 : 23, 35, 39, 51; *Upogebia* (*Upogebia*) *spinigera* de Man, 1928 : 29, 39, 45; *Upogebia* (*Upogebia*) *sturgisae* Boone, 1931 : 161, fig. 11; *Upogebia spinigera* Holthuis, 1952 : 1–11, figs 1, 2.

MATERIAL EXAMINED. Rio Tumbler (Rio Tumbes, Peru ?), 1890, 3 ♂♂, c.l. 10–12 mm, t.l. 31–36 mm; 6 ♀♀ (5 ovigerous), c.l. 9–12 mm, t.l. 29–40 mm.
St Lucia, Peru, 1890, 1 ♂, c.l. 11 mm, t.l. 36 mm.
West Coast of Central America, 1875, 1 ♂, c.l. 10 mm, t.l. 31 mm; 2 ♀♀ (1 ovigerous), c.l. 8 mm, 10 mm, t.l. 26 mm, 30 mm.
Esmeraldas, Ecuador, 1925, 2 ♂♂, c.l. 8 mm, 10 mm, t.l. 25 mm, 31 mm; 2 ♀♀ (1 ovigerous), c.l. 10 mm, 12 mm, t.l. 33 mm, 42 mm.

REMARKS. The present material has been compared with the two specimens of *U. spinigera* described by Holthuis (1952). Table 3 lists the main variations observed.

Table 3 Variations in the material of *U. spinigera* from areas of Central and South America

	Material from Colombia	Material from W. coast of Central America	Material from St Lucia, Peru	Material from Rio Tumbler	Material from Esmeraldas, Ecuador
Number of specimens examined	2	3	1	9	4
Spines on hind margin of cervical groove	present, large	present, large	present, small	present, small	present in 2 specimens
Spines on anterior margin of carpus of pereiopod 2	present, large	present in 2 specimens	present, small	present in 4 specimens	present
Spines on upper margin of carpus and merus of pereiopod 2 and 4	present, small and transparent	absent	absent	absent	absent
Spines on lower margin of merus of pereiopod 3	present	present	present	present	present
Spines on lower margin of merus of pereiopod 4	present	present in 2 specimens	absent	absent	absent
Coxal spines on pereiopods 1–3	present	present on pereiopods 2 and 3	absent	present on pereiopod 3	present

1. Spines on the lateral part of the cervical groove, which are apparent in the material from Colombia, are much smaller in the present material and are missing in two specimens (1 ♂, 1 ♀) from Ecuador.

2. The subterminal spine of the cheliped dactylus is large in the present material and usually larger than that of the specimens from Colombia. In some specimens, the cheliped fixed finger is nearly as long as the dactylus. The cheliped of the material from Colombia was illustrated by Holthuis (1952) and that figure seems to represent the inner side of the appendage. The description of the outer side of the cheliped would correspond in fact to the inner side and *vice versa*. The inner and outer side of the left cheliped of the ovigerous female from the West Coast of Central America are here illustrated (Fig. 3g, h).

3. Both the upper and the lower margin of the carpus of the second pereiopod bear a spine distally. These two spines are large in the Colombia specimens but small or absent in the present material.

4. Small and transparent spines are present on the upper margin of the carpus and merus of the third and fourth pereiopods of the Colombia specimens but are absent in the present material. They are not mentioned either in the original description of the species by Smith (1871) and Holthuis (1952) thought they were overlooked by the former author. Since none of the present specimens has got these spines, they may in fact be absent in Smith's material also.

5. Smith (1871), Boone (1931) and Holthuis (1952) mention that the lower margin of the third and fourth pereiopods is armed with spines whilst Streets (1871) states that these segments are unarmed. In the present material, the lower margin of the merus of the third pereiopod is armed in all specimens but in most of them, the same margin of the fourth pereiopod is unarmed.

6. The presence of coxal spines on the 1st–3rd pereiopod is subject to variation among specimens of the present material. Coxal spines are absent from the fourth pereiopod and are present on the fifth pereiopod in all specimens of the present material as well as that from Colombia.

DISTRIBUTION. Gulf of Fonseca, N.W. Nicaragua; Aseredoras Island, W. Nicaragua (Smith, 1871). Isthmus of Panama (Streets, 1871). Fernando Noronha, N.E. Brazil (Pocock, 1890). Patillo Point, Panama (Boone, 1931). Colombia (Holthuis, 1952). Rio Tumbler; St Lucia, Peru; Esmeraldas, Ecuador.

Acknowledgements

I wish to thank the Trustees of the British Museum (Natural History) for allowing me the opportunity to examine their collections and for the working facilities provided, Dr R. W. Ingle for kindly supervising my research and for critically reading the manuscript. I also wish to thank the Directors of the Rijksmuseum van Natuurlijke Historie, Leiden; Instituut voor Taxonomische Zoologie, Amsterdam; Naturhistoriska Riksmuseet, Stockholm; and the Zoological Survey of India, Calcutta for sending material for examination; Mme M. de Saint Laurent, Muséum national d'Histoire naturelle, Paris for her advice, and Danida (Danish International Development Agency) for the financial support received during part of the work.

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Manuscript accepted for publication 9 June, 1977

Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 2. *Palaemonetes (Palaemonetes) varians* (Leach, 1814) and morphological variation

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Synopsis

Five larval and selected post larval stages of *Palaemonetes* (*Palaemonetes*) *varians* are described from specimens reared in the laboratory. The rate of larval development and the effect of desynchronization of epigenesis and moulting are discussed. Analysis of morphometric and meristic variation showed that normalizing selection may result in a reduction in variation of larval size distribution at metamorphosis. No such reduction in variation of meristic characters was found. A significant increase in variation of the exopodite of the mouthpart maxilla 2 was recorded from the closely related palaemonid *Palaemon* (*Palaeander*) *elegans*. The significance of these results is discussed with reference to the life histories of these shrimps.

Introduction

Palaemonetes (*Palaemonetes*) *varians* or the ditch shrimp has been the subject of larval development studies for nearly 140 years (see synopsis of larval data, below). The species is reared easily in the laboratory and this explains, to some extent, its popularity. It was cited as an example of poecilogony (Boas, 1889) or larval polymorphism, until Sollaud (1923*a*) showed that there were, in fact, different species in northern and southern Europe and in North Africa but that co-existence occurred. Heldt (1953) revived the controversy after examining samples of *P.* (*P.*) *varians* from Lake Kelbia in Tunis. In different salinities Heldt reported that '. . . ces larves différentes, issues de ces deux sortes d'œufs, aboutissent . . . à des adultes morphologiquement identiques'. It is, however, not difficult to see why the concept of poecilogony has been applied to this species which does, apparently, show considerable phenotypic variation during larval development and metamorphosis.

A species is often characterized solely by genotype and phenotype in discussions on development. Waddington (1953) developed a further concept – the *epigenotype* which he defined as '. . . the system of causal relations by which the newly fertilized zygote . . . becomes realized as the fully developed adult'. He distinguished between normalizing selection in which phenotypes resulting directly from the presence of an abnormal gene were removed from a population, and stabilizing selection which involved the removal of phenotypes disadvantaged by an unstable epigenetic system.

In this context morphometric and meristic data for larval stages of *Palaemonetes* (*Palaemonetes*) *varians* were pooled and analysed to see if epigenetic development in shrimps followed the same pattern reported recently in the development of newts (Bell, 1974, 1975), when a decrease in morphological variation was recorded as the animals approached metamorphosis.

Materials and methods

Rearing

Ovigerous *Palaemonetes* (*Palaemonetes*) *varians* (Leach) were collected in July 1976 by handnetting from ditches alongside the estuary at Burnham-on-Crouch, Essex, England (grid reference

Bull. Br. Mus. nat. Hist. (Zool.) **35** (2): 127–200

Issued 26 April, 1979

TQ 943957). Rearing techniques, similar to those reported previously (Fincham, 1977), were used with the following modifications:

1. The constant temperature room was at 22 ± 0·5 °C; 2 °C below the temperature of the water in the ditches where the collections were made.
2. No mass cultures were set up in order to eliminate the problems of identifying later zoeal stages where moulting history was not available. To ensure, however, that adequate material was available for drawing and assessing morphological variation, eight compartmented trays were set up, containing 144 larvae. At each zoeal stage, 10 larvae, their moults, and a further 10 moults from other individuals, were preserved.
3. All trays and equipment were sterilized with boiling water before use to prevent the accumulation of bacteria.

Larval material has been deposited in the Crustacea collection of the BM(NH), registration number 1977 : 284.

Analysis of morphometric and meristic variation

Ten moults and larvae were examined at each stage to determine the range of overall size and also of setal numbers on selected appendages. Mean ($\bar{x}$) and standard deviation (*s.d.*) were calculated for each character at the different stages. To test if there was a genuine increase in variation other than an increase expected from animals of greater size, coefficients of variation (100 × *s.d.*/mean) were calculated.

Palaemonetes* (*Palaemonetes*) *varians (Leach, 1814)

Palaemon varians Leach, 1814.
Palaemon variabilis Bouchard-Chantereaux, 1829.
Palaemonetes varians microgenitor Boas, 1889.
Palaemonetes varians occidentalis Sollaud, 1923.
Palaemonetes (*Palaemonetes*) *varians* Holthuis, 1949.

SYNOPSIS OF LARVAL DATA FROM PUBLISHED WORK. *Palaemon variabilis*: Du Cane, 1839 (zoeae 1–4, dorsal, lateral views, plankton, British waters); *Palaemonetes varians*: Boas, 1880 (selected appendages of some zoeae, Danish waters); Mayer, 1880 (zoeae 1–4, post larvae, some dorsal, lateral views, appendages, Mediterranean waters); Weldon, 1890 (zoeae 1–3/4, no figures, laboratory reared, British waters); Allen, 1893*a*, *b* (development of green gland, shell gland and body cavity in larvae, laboratory reared, British waters); *P. v. microgenitor*: Sollaud, 1914 (egg size, abbreviated development and order of appendage appearance); Sollaud, 1919 (effect of environment on duration of larval life, French waters); Sollaud, 1921 (phototropism before and after metamorphosis); *P. varians*: Gurney, 1923 (breeding period, British waters); *P. v. occidentalis*: Sollaud, 1923*a* (zoeae 1–5, post larva, French waters); 1923*b* (larval polymorphism); *P. varians*: Gurney, 1924 (zoeae 1–5, post larvae, plankton and laboratory reared, British waters); Sollaud, 1930 (larval polymorphism); Heldt, 1953 (larval polymorphism); Weygoldt, 1961 (embryology, German waters); Le Roux, 1970 (effect of environment on number of larval stages, French waters).

In the following short descriptions of the key characters of the larval stages, all setal counts have been omitted but these are recorded in Table 1.

DESCRIPTION OF LARVAL STAGES
Key characters are printed in *italic type*.

ZOEA 1 (Fig. 1) 3·8 mm (3·5–4·1 mm)

Head (Figs 1a, b): *eyes sessile*.

Carapace (Figs 1a, b): *without spines*, rostrum straight, tapering distally, ventral margin with minute retrorse teeth distally.

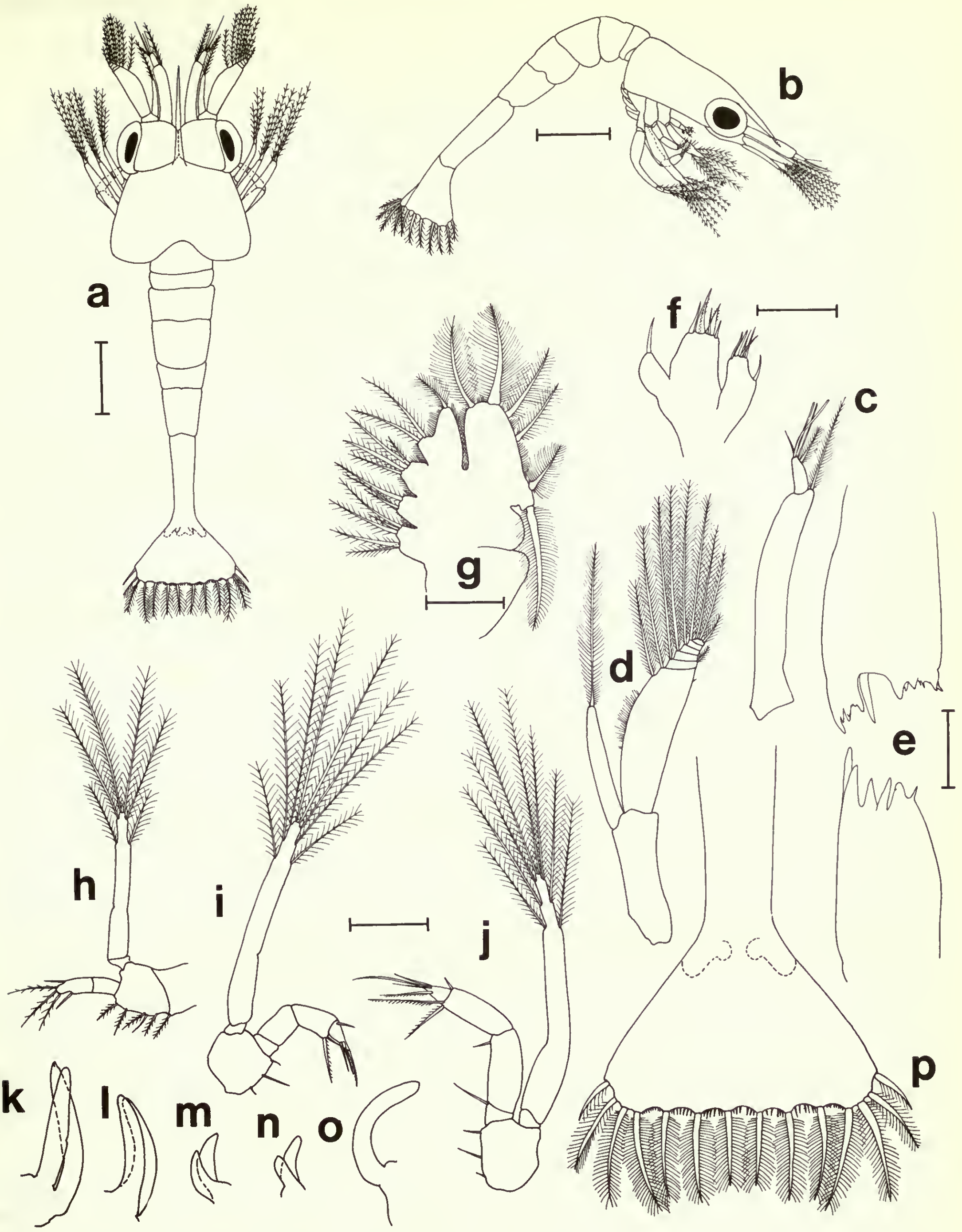

Fig. 1 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; g = 0·1 mm; e, f = 0·05 mm.

Antenna 1 (Fig. 1c): peduncle bearing single flagellar segment with three aesthetascs distally, one wider than the others.*

Antenna 2 (Fig. 1d): exopodite as a broad lamina divided into 5 short segments distally.

Mandibles (Fig. 1e): asymmetrical.

Maxillipeds 1–3 (Figs 1h–j): with natatory exopodites.

Pereiopods 1–4 (Figs 1k–n): *rudimentary, biramous.*

Pereiopod 5 (Fig. 1o): *rudimentary, uniramous.*

Abdomen (Figs 1a, b): somite 6 continuous with telson; pairs of ventral buds on somites 1–5 indicate position of pleopods.

Telson (Fig. 1p): fans out distally, posterior margin bears 7+7 plumose spines, with minute spines between four innermost pairs of spines.

ZOEA 2 (Fig. 2) 4·2 mm (4·0–4·5 mm)

Head (Figs 2a, b): *eyes 'stalked'.*

Carapace (Figs 2a, b): one *dorso-medial* and a pair of supraorbital spines all bent forward with small retrorse teeth ventrally, rostrum without teeth.

Antenna 1 (Fig. 2c): distal segment of peduncle bearing first segment of internal flagellum, external flagellum now with four distal aesthetascs, two wider than others.

Pereiopods 1, 2 (Figs 2k, l): *developed, with natatory exopodites.*

Pereiopods 3, 4 (Figs 2m, n): *rudimentary, biramous.*

Pereiopod 5 (Fig. 2o): *developed, uniramous* (without exopodite).

Abdomen (Figs 2a, b): *somite 5 with posterior margin produced into a pair of spines.*

Telson (Fig. 2p): *developing uropods visible beneath exoskeleton*; in central group of small spines, one pair longer than the others.

ZOEA 3 (Fig. 3) 4·6 mm (4·3–4·8 mm)

Carapace (Figs 3a, b): *two dorso-medial spines* and a small frontolateral spine at edge of carapace beneath the eyes, former with retrorse teeth ventrally.

Antenna 1 (Fig. 3c): external flagellum with three distal aesthetascs; conspicuous spine medially and stylocerite forming on proximal external margin of first segment of peduncle.

Antenna 2 (Fig. 3d): exopodite with distal part divided into only three short segments.

Pereiopods 1, 2 (Figs 3k, l): endopodite with internal distal margin of propodus produced slightly forward (will become fixed finger of chela).

Pereiopod 3 (Fig. 3m): *developed, with natatory exopodite.*

Abdomen (Figs 3a, b): *somite six divided from telson by suture.*

Telson (Fig. 3p): narrower, but still broader distally, outer pair of spines on posterior margin considerably reduced: *uropod endopodite with no marginal setae*; *exopodite with marginal, plumose setae.*

ZOEA 4 (Figs 4, 5) 5·2 mm (4·9–5·5 mm)

Carapace (Figs 4a, b): *three dorso-medial spines* with small retrorse teeth ventrally.

Antenna 2 (Fig. 5b): endopodite with 3-segmented flagellum (usually), as long as scaphocerite, distal part of exopodite divided into two, one or no short segments.

Pereiopods 1, 2 (Figs 5f, g): *endopodite with internal distal margin of propodus* produced forward to over half length of dactylus (excluding terminal setae).

Pereiopod 4 (Fig. 5i): developed with natatory exopodite.

Abdomen (Figs 4b, 5k–o): pleopods on somites 1–5 rudimentary, biramous.

Telson (Fig. 5p): a little broader distally than proximally, posterior margin weakly concave with *5+5 large spines* and with 2 smaller spines on latero-distal margin; *endopodite and exopodite of uropod both with marginal plumose setae.*

ZOEA 5 (Figs 6, 7, 8) 5·8 mm (5·5–6·0 mm)

Carapace (Fig. 6b): *setae in angles of two anterior dorso-medial spines.*

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* In a previous paper (Fincham, 1977) two aesthetascs were recorded distally on the flagellar segment of antenna 1 in zoea 1 of *Palaemon* (*Palaeander*) *elegans*. Examination of more material, including specimens from the Marmara Sea, Turkey, indicate that three aesthetascs is the usual number (one wide, two narrow).

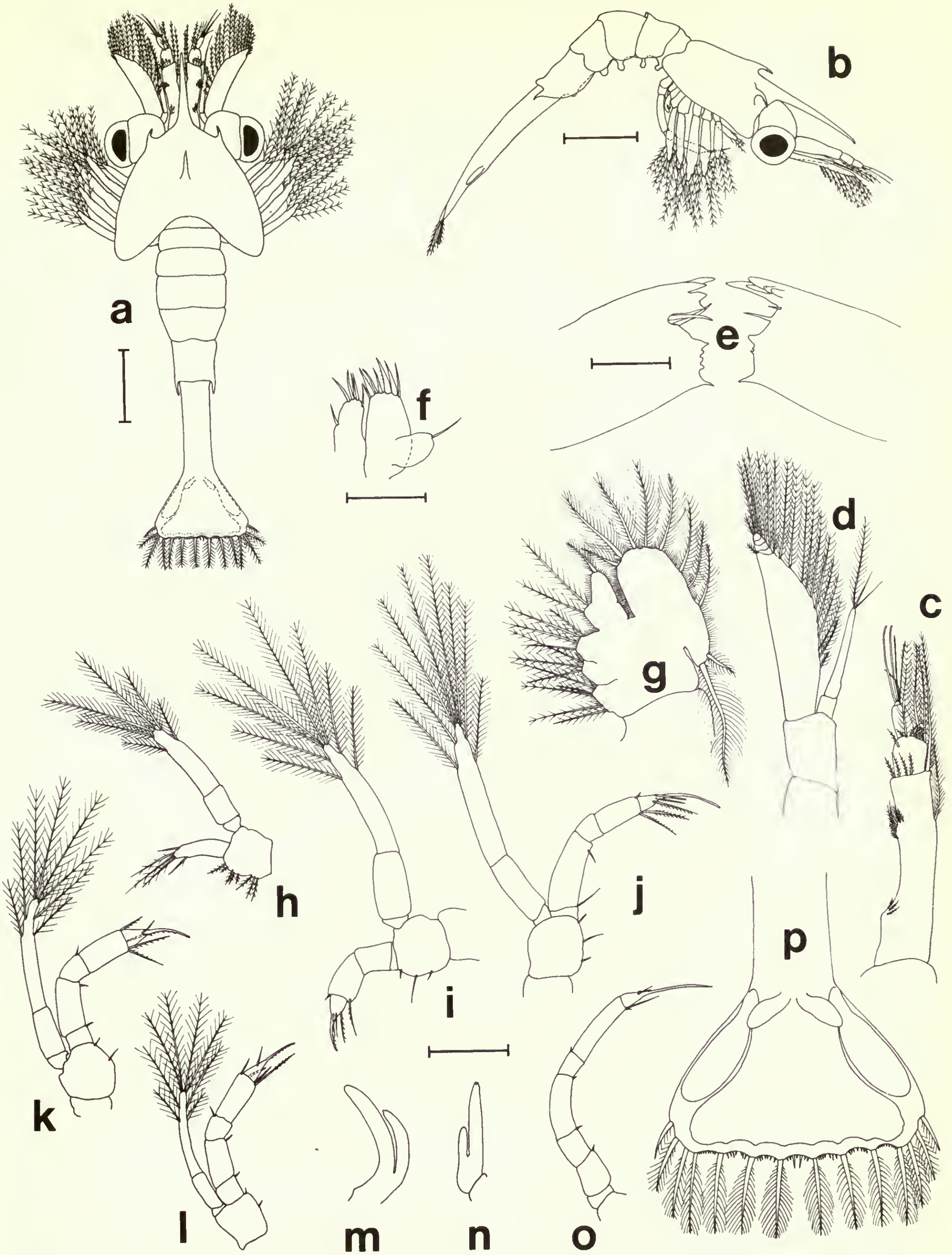

Fig. 2 Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; f, g = 0·1 mm; e = 0·05 mm.

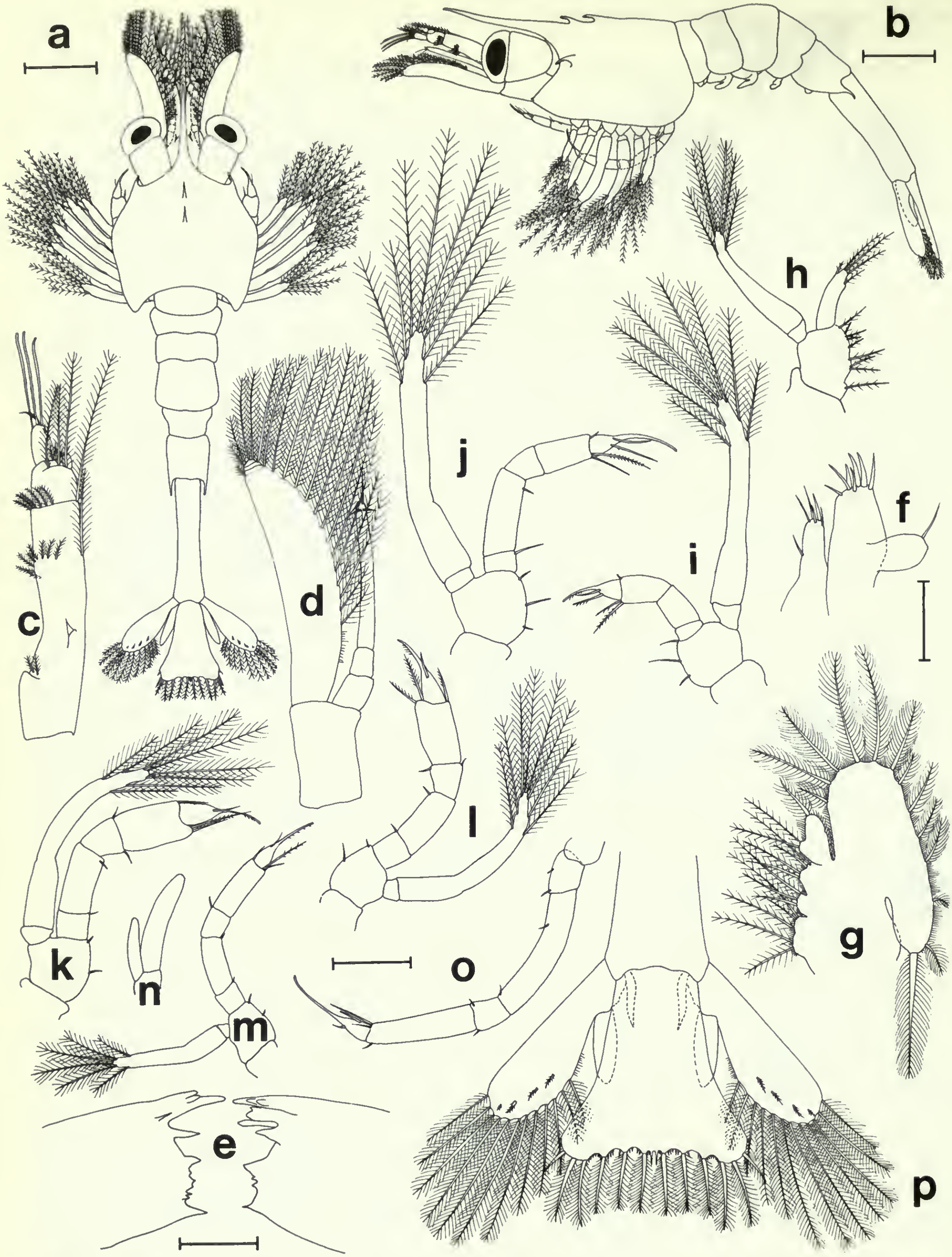

Fig. 3 Zoea 3: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; f, g = 0·1 mm; e = 0·05 mm.

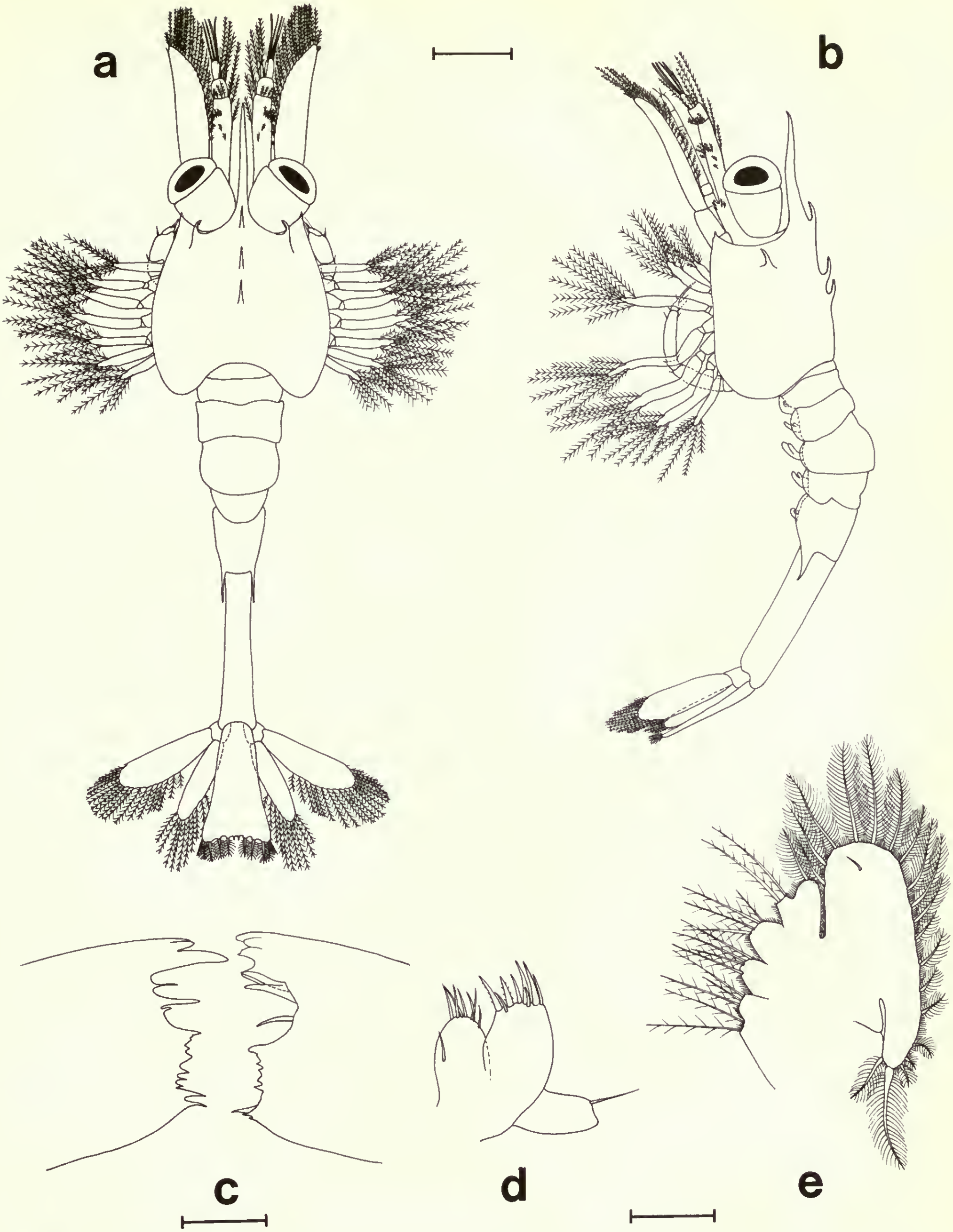

Fig. 4 Zoea 4: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm.

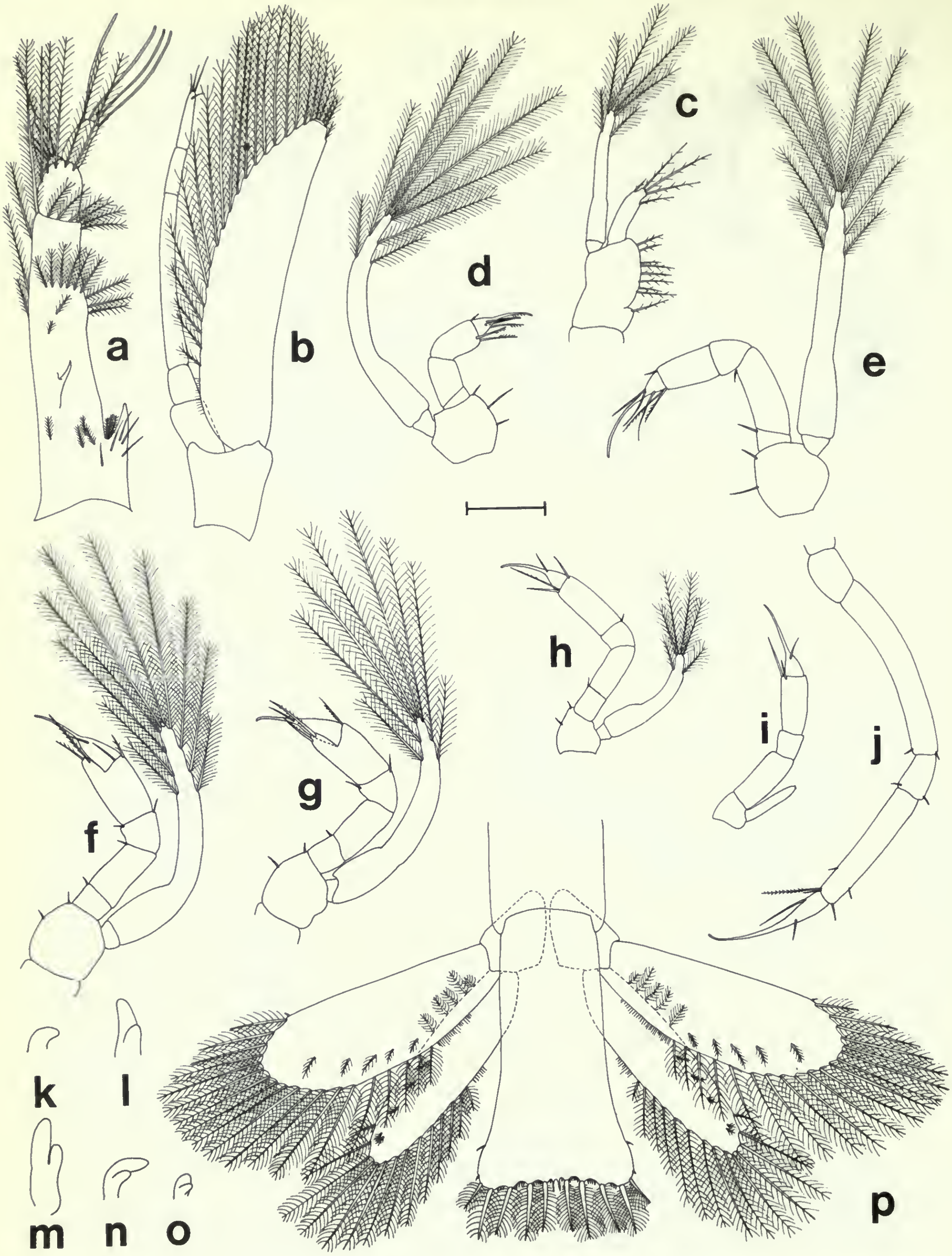

Fig. 5 Zoea 4: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) pleopod 1; (l) pleopod 2; (m) pleopod 3; (n) pleopod 4; (o) pleopod 5; (p) telson. Bar scale: a–p = 0·2 mm.

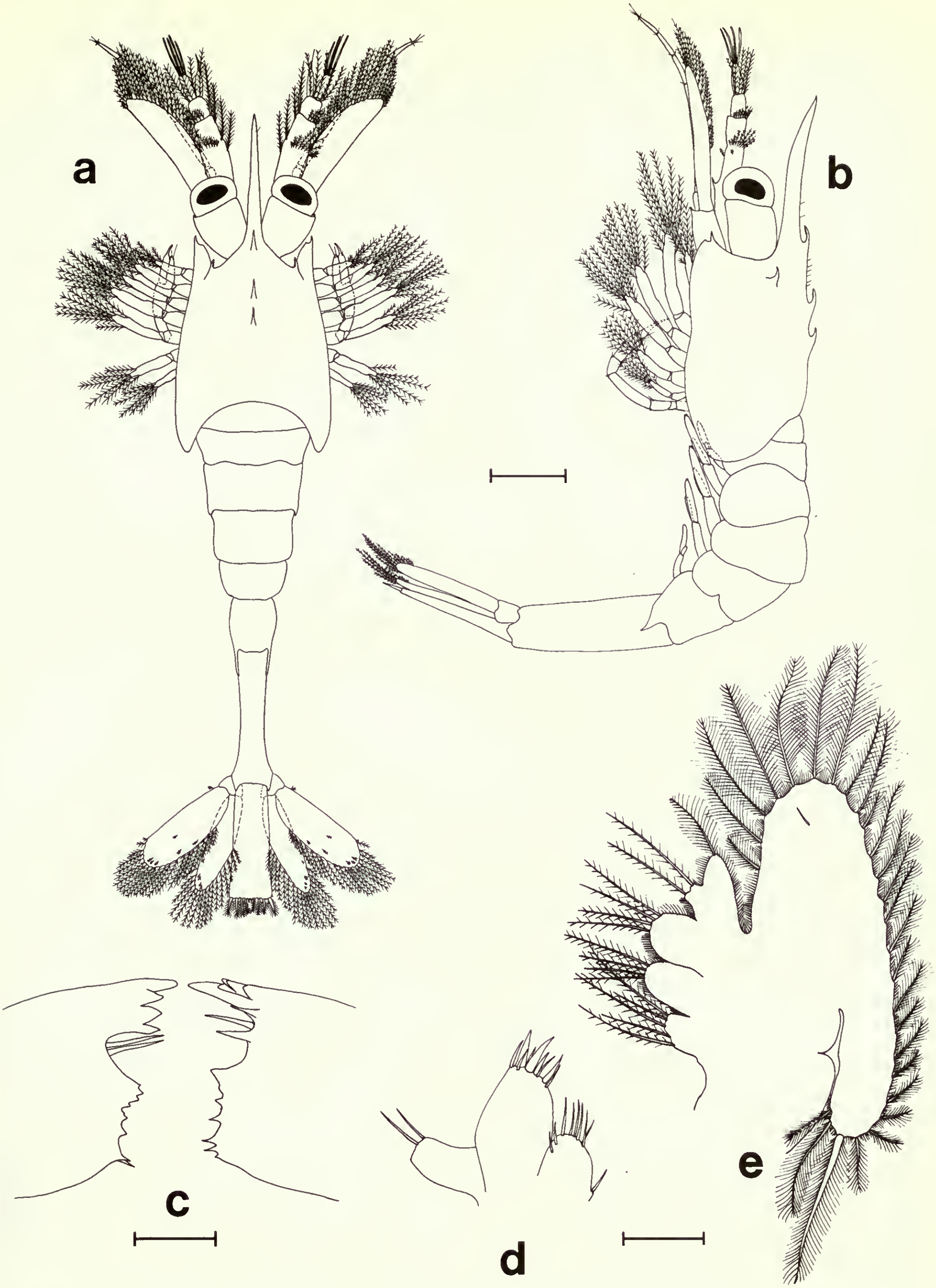

Fig. 6 Zoea 5: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm.

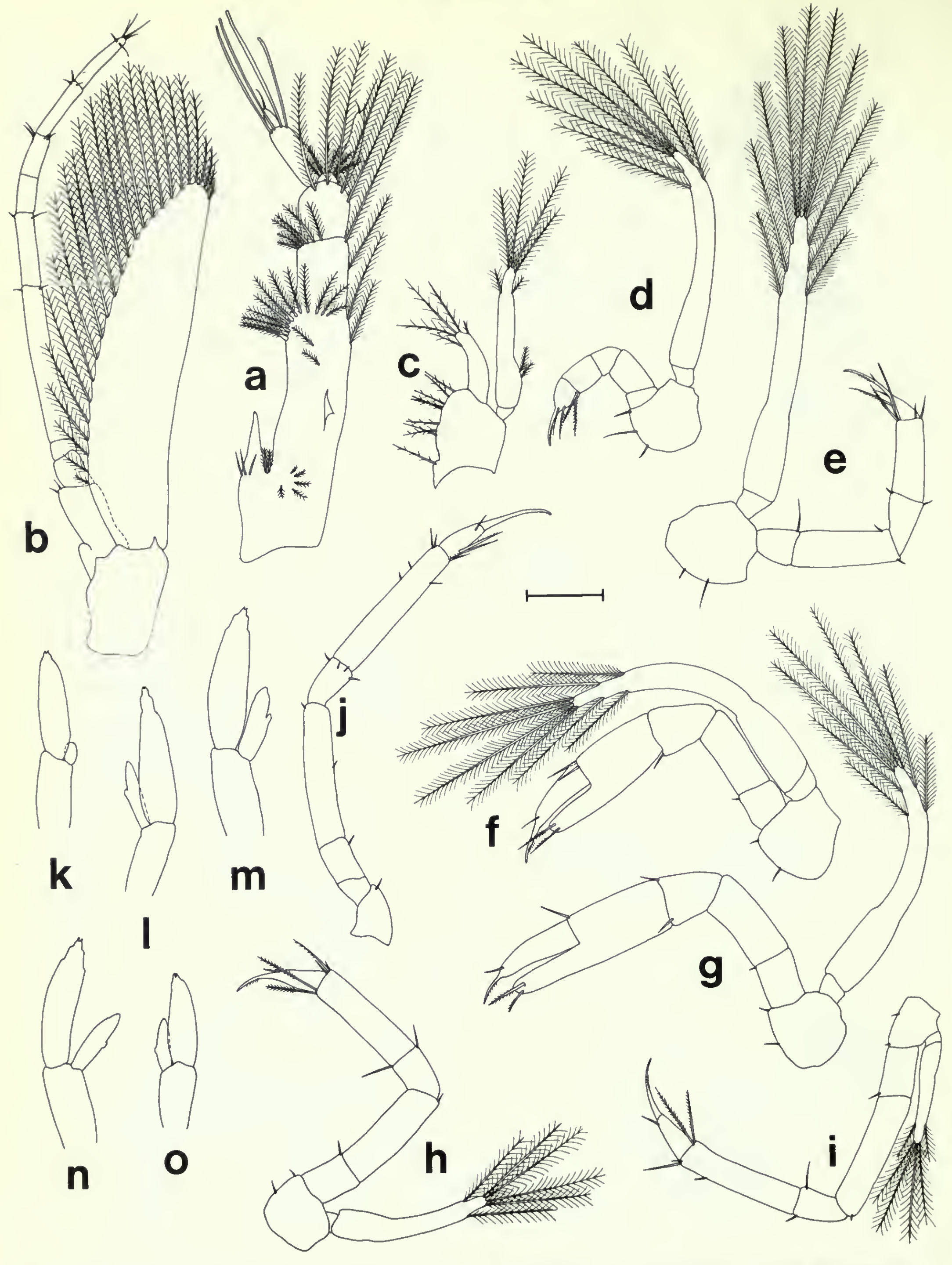

Fig. 7 Zoea 5: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) pleopod 1; (l) pleopod 2; (m) pleopod 3; (n) pleopod 4; (o) pleopod 5. Bar scale: a–o = 0·2 mm.

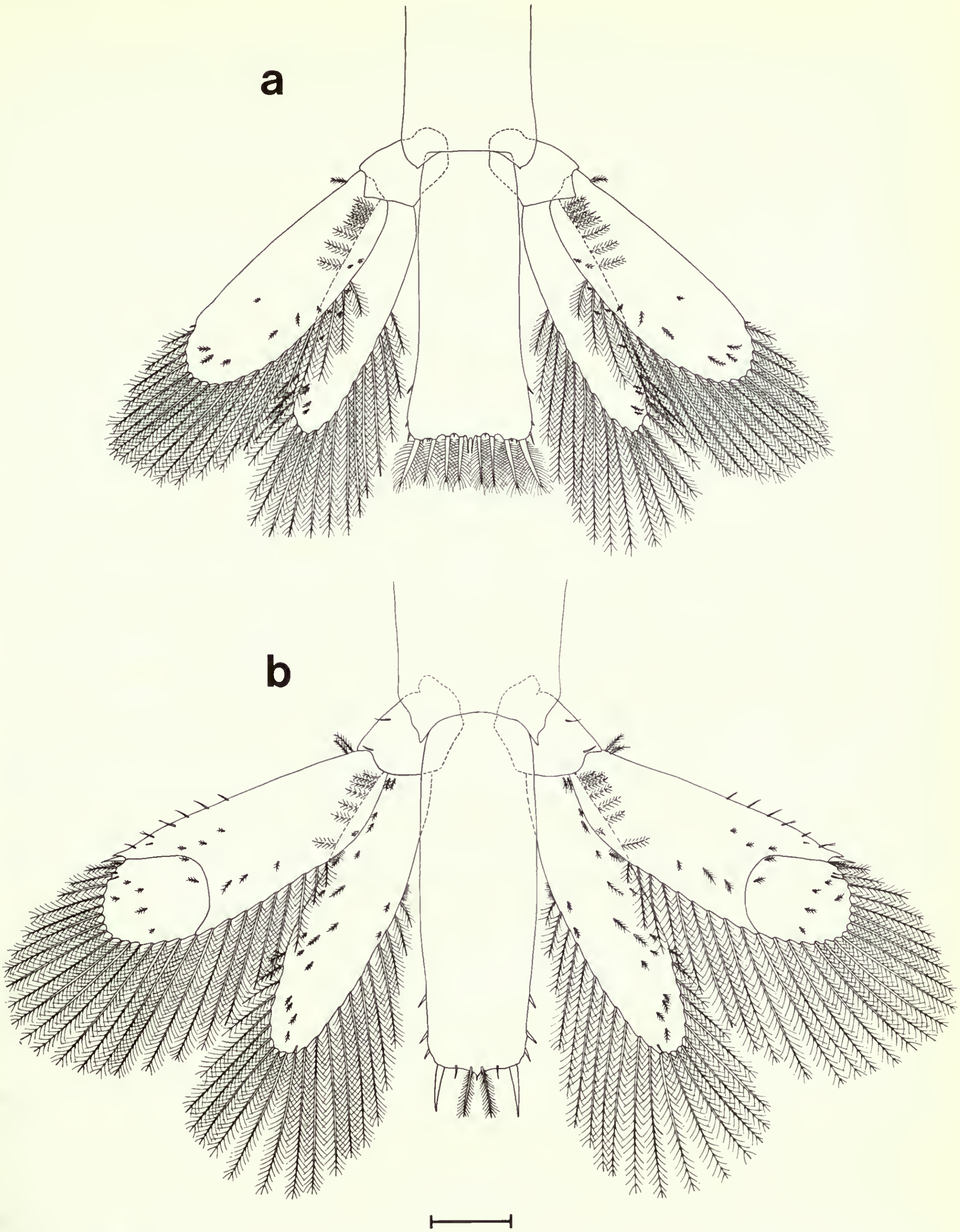

Fig. 8 Zoea 5: (a) telson. Post larva 1: (b) telson. Bar scale: a, b = 0·2 mm.

Antenna (Fig. 7a): circlet of plumose setae developed dorsally on first segment of peduncle, indicating position of statocyst.

Antenna 2 (Fig. 7b): *increase in number of segments of endopodite flagellum, just longer than scaphocerite.*

Pereiopods 1, 2 (Figs 7f, g): *endopodite with immovable finger of propodus produced forward to almost length of dactylus* (excluding terminal setae).

Abdomen (Figs 6a, b, 7k–o): *pleopods with rudimentary setae on margins of exopodite, endopodite of pleopods 2–5 with rudiment of appendix interna* (*stylamblys*).

Telson (Fig. 8a): further narrowing distally, posterior margin still weakly concave with *4+4 large spines* and with 3 smaller spines on latero-distal margin.

POST LARVA 1 (Figs 8, 9, 10, 11) 6·4 mm (6·0–7·0 mm)

Carapace (Figs 9a, b): *rostrum with 3–6 dorsal and 1–2 ventral spines, supraorbital spines missing.*

Antenna 1 (Fig. 10a): internal flagellum of 2–4 segments and usually an additional group of 2 aesthetascs distally on first segment of external flagellum.

Antenna 2 (Fig. 10b): endopodite with flagellum multisegmented, more than twice length of scaphocerite.

Mandible (Fig. 9c): *divided into pars incisiva and pars molaris*, lacinia mobilis no longer present.

Maxilliped 2 (Fig. 10d): endopodite with dactylus, propodus and merus flattened, *exopodite shortened and with no setae.*

Maxilliped 3 (Fig. 10e): endopodite dactylus shortened, *exopodite reduced* to less than half length of endopodite, and without setae.

Pereiopods 1, 2 (Figs 10f, g): ischium, merus and carpus lengthened, *exopodite reduced* to about the length of the ischium of endopodite and with no setae.

Pereiopods 3, 4 (Figs 10h, i): endopodite dactylus evenly tapering distally, propodus, carpus and merus lengthened, *exopodite reduced*, extending halfway along ischium of endopodite, setae generally absent but with a few small, plumose setae sometimes present.

Pereipod 5 (Fig. 10j): dactylus evenly tapering distally, other segments of endopodite lengthened.

Pleopod 1 (Fig. 11a): ratio of endopodite to exopodite 1 : 4, *endopodite bearing terminal plumose setae, exopodite fringed with long plumose setae.*

Pleopods 2–5 (Figs 11b–e): endopodite over half length of exopodite, both with long, marginal, plumose setae, endopodite with appendix interna bearing well-developed intero-distal coupling hooks.

Telson (Fig. 8b): *narrow, posterior margin convex with a short, median point, 1+1 large spines* and two pairs of setae on the posterior margin, one long and plumose, other simple, also 3 smaller spines on latero-distal margin.

POST LARVA 2 (Fig. 11) 7·2 mm (6·8–7·9 mm)

Maxillipeds, 2, 3: exopodites lengthen and regain marginal, plumose setae.

Pereiopods 1–4: exopodites continue to diminish.

Telson (Fig. 11g): extremely narrow, median point on posterior margin more pronounced.

POST LARVA 5 (Fig. 11)

Antenna 1 (Fig. 11h): development of accessory flagellum on external flagellum.

Antenna 2 (Fig. 11i): morphogenesis of exopodite complete – truncated distally, edges almost parallel.

Discussion

Results of the present study are summarized in Tables 1 and 2. The temporary regression of the exopodites of maxillipeds 2 and 3, in which shortening occurred with loss of marginal plumose setae and also the disappearance of the natatory exopodites of pereiopods 1–4, paralleled exactly the changes at first post larval moult (PL 1) for *Palaemon* (*Palaeander*) *elegans* (Fincham, 1977). The relatively abbreviated development of *Palaemonetes* (*Palaemonetes*) *varians* compared with the 6–9 stages of *Palaemon* (*Palaeander*) *elegans* is accompanied by a change in the sequence of

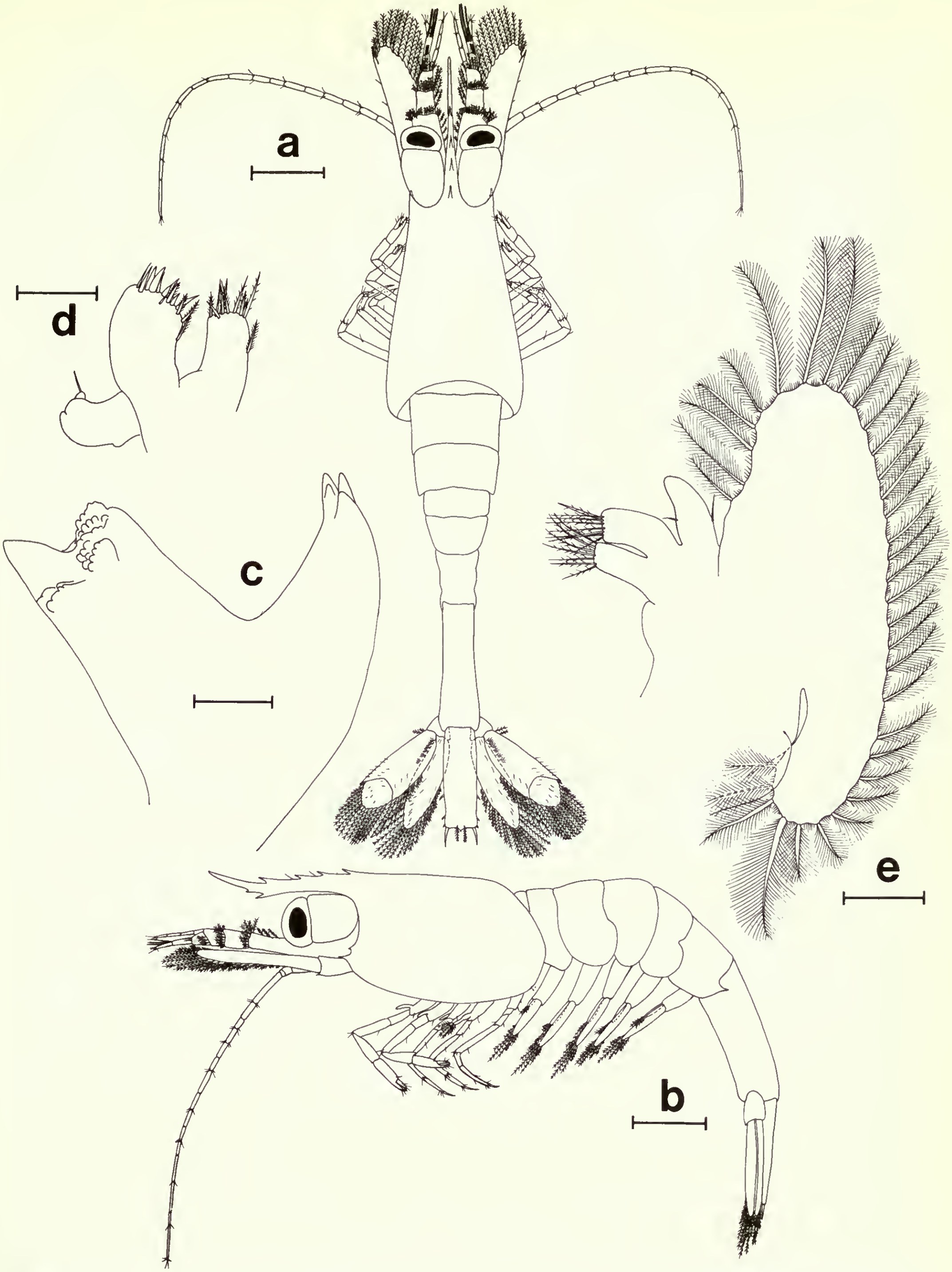

Fig. 9 Post larva 1: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm.

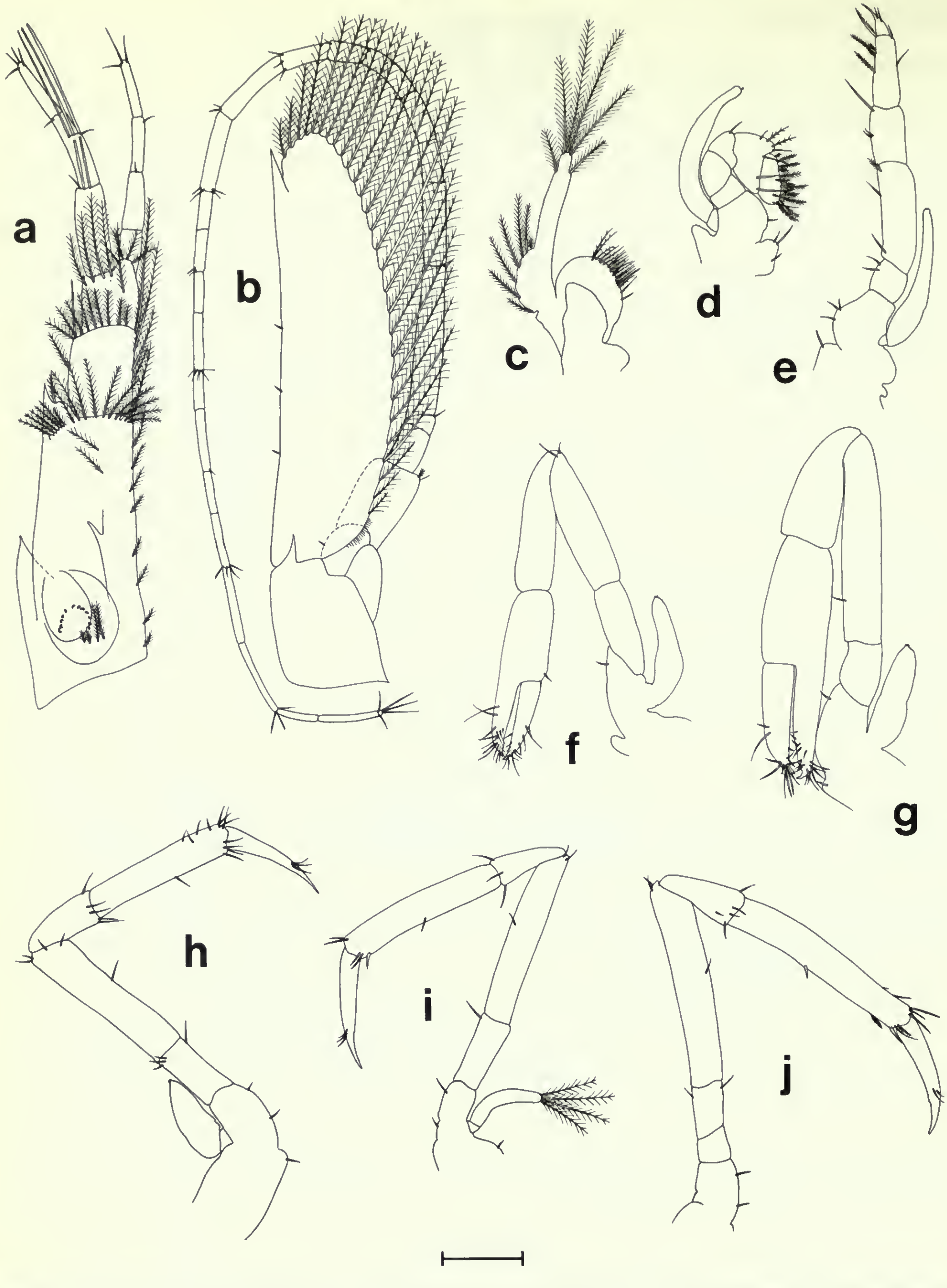

Fig. 10 Post larva 1: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5. Bar scale: a–j = 0·2 mm.

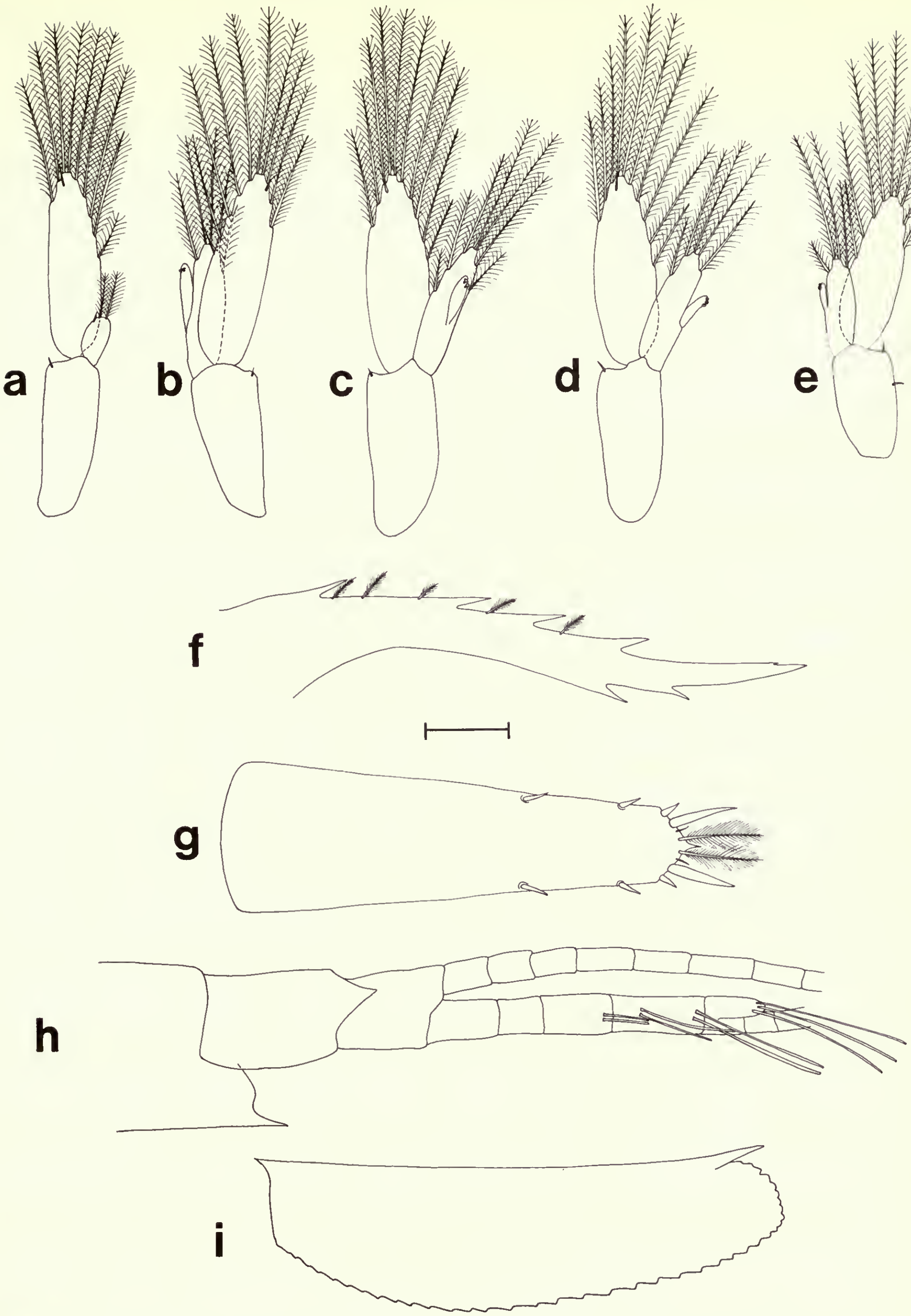

Fig. 11 Post larva 1: (a) pleopod 1; (b) pleopod 2; (c) pleopod 3; (d) pleopod 4; (e) pleopod 5. Post larva 2: (f) rostrum; (g) telson. Post larva 5: (h) antenna 1 (aesthetascs drawn, setae omitted); (i) antenna 2 (setae omitted.) Bar scale: a–i = 0·2 mm.

Table 1 Larval development and range of morphological variation in *Palaemonetes* (*Palaemonetes*) *varians*

		Zoea/Stage					
		1	2	3	4	5	PL1
Length (mm)	Mean	3·8	4·2	4·6	5·2	5·8	6·4
	Range	(3·5–4·1)	(4·0–4·5)	(4·3–4·8)	(4·9–5·5)	(5·5–6·0)	(6·0–7·0)
Carapace							
No. of dorsal spines		0	1	2	3	3	3–5
No. of ventral rostral spines		0	0	0	0	0	1–2
Supraorbital spines +/−		−	+	+	+	+	−
No. of antero-lateral spines		0	0	1	1	1	2
Rostrum tip – Ventral retrose hooks +/−		+	−	−	−	−	−
Antenna 1							
No. of groups, aesthetascs		1	1	1	1	1	1–2
Stylocerite +/−		−	+/−	+	+	+	+
Statocyst +/−		−	−	−	−	−	+
Medial spine +/−		−	−	+	+	+	+
No. of segments, flagellum – Internal		0	1	1	1	1	2–4
External		1	1	1	1	2	3–4
Accessory flagellum +/−		−	−	−	−	−	−
Antenna 2							
Endopodite – No. of segments		1	2	3	5	7–10	16–28
c.f. Length of scaphocerite		0·50	0·50	0·66–0·75	1·0–1·25	1·50–1·75	2·0+
Exopodite – No. of distal segments		5	4	2	0	0	0
No. of plumose setae		9	16–18	18–21	21–23	23–26	24–32
External spine +/−		−	−	−	−	−	+
Mandible – Lacinia mobilis +/−		+	+	+	+	+	−
Maxilla 1							
No. of endite setae – Coxa		5–6	6	6–7	6–8	8–9	11
Basis		5–6	7	7–8	8–9	9	14
Maxilla 2							
No. of endite setae – Coxa		4–5	4–5	5	5–6	5	2
Basis 1		3	3	3	3–4	4–5	8
Basis 2		4	4	4	4	4–5	7
Endopodite		3–4	3–4	3	3	3–4	0
No. of plumose setae Exopodite		5–6	10–12	12–15	19–21	26–29	29–35
Maxilliped 1							
No. of setae on internal margin – Basis		5	8	9	9	9	19
Exopodite – No. of setae – Lateral (proximal)		0	0	0	0	2	7

pereiopod development. Limb buds were present in zoea 1, and at zoea 2 only pereiopods 3 and 4 were still rudimentary. At zoea 3 pereiopod 3 was fully developed together with a functional natatory exopodite, and at zoea 4 pereiopod 4 was fully formed also. The change to adult-type mandible (Fig. 9c) is made at the moult to PL 1 and is associated with the change in diet necessitated by the major behavioural change from a planktonic to largely benthic existence.

Table 1 (*cont.*)

		Zoea/Stage					
		1	2	3	4	5	PL1
Length (mm)	Mean Range	3·8 (3·5–4·1)	4·2 (4·0–4·5)	4·6 (4·3–4·8)	5·2 (4·9–5·5)	5·8 (5·5–6·0)	6·4 (6·0–7·0)
Maxilliped 2							
Endopodite – No. of segments		4	4	4	4	5	5
Exopodite +/−		+	+	+	+	+	+
Setae +/−		+	+	+	+	+	−
Maxilliped 3							
Endopodite – No. of segments		4	5	5	5	5	5
Exopodite +/−		+	+	+	+	+	+
Setae +/−		+	+	+	+	+	−
Pereiopods 1 & 2 +/−		R+	+	+	+	+	+
Biramous +/−		+	+	+	+	+	R+
Endopodite – Propodus fixed finger +/−		−	−	+	+	+	+
Pereiopod 3 +/−		R+	R+	+	+	+	+
Biramous +/−		+	+	+	+	+	R+
Pereiopod 4 +/−		R+	R+	R+	+	+	+
Biramous +/−		+	+	+	+	+	R+
Pereiopod 5 +/−		R+	+	+	+	+	+
Biramous +/−		−	−	−	−	−	−
Abdomen							
Somite 5 – Lateral spines +/−		−	+	+	+	+	+/−
Somite 6 – Continuous with telson +/−		+	+	−	−	−	−
Pleopods +/−		R+	R+	R+	R+	+	+
Fringing setae		−	−	−	−	−	+
Appendix interna 2–5 +/−		−	−	−	−	R+	+
Telson							
Posterior margin concave (−) convex (+)		+/−	+/−	−	−	+/−	+
Spine formula		7+7	7+7	6+6	5+5	4+4	1+1 (PL2:2+2)
Small spines +/−		+	+	+	+	+	−
No. of pairs – Lateral spines		0	0	1	2	3	3 (PL2:2)
Uropods +/−		−	−	+	+	+	+
Long plumose setae – Endopodite				0	10–14	16–18	18–22
Exopodite				11–13	17–20	20–23	21–26

Rate of epigenesis

In order to transform zoea 1 to a miniature adult or juvenile, a definite sequence of morphogenetic and associated biochemical and physiological development and adaptation has to be completed. If larvae moult 'early', less of the developmental sequence is completed. Epigenesis in Crustacea is a continuous sequential process despite being apparently arrested at morphological

Table 2 Analysis of morphometric variation (a) in overall size in mm and meristic variation in the number of expodite plumose setae of (b) antenna 2, (c) uropod and (d) maxilla 2 during the development to post larva of *Palaemonetes* (*Palaemonetes*) *varians* (n.d. = not developed; see Materials and Methods for statistical abbreviations)

		Stage					
		1	2	3	4	5	PL1
a	$\bar{x}$	3·82	4·24	4·55	5·19	5·77	6·41
	s.d.	0·21	0·18	0·14	0·17	0·18	0·32
	c. of v.	5·49	4·19	3·15	3·20	3·06	5·01
b	$\bar{x}$	9	17·0	19·5	22·3	25·2	27·4
	s.d.	0	0·82	1·08	0·67	0·92	2·37
	c. of v.	0	4·80	5·54	3·03	3·65	8·64
c	$\bar{x}$	n.d.	n.d.	12·2	18·6	21·6	23·7
	s.d.	–	–	0·79	0·97	1·26	1·64
	c. of v.	–	–	6·47	5·19	5·86	6·90
d	$\bar{x}$	5·6	10·6	13·4	19·7	27·5	31·7
	s.d.	0·52	0·70	1·17	0·67	1·35	2·06
	c. of v.	9·22	6·60	8·76	3·43	4·92	6·49

stages during the intermoult period of ecdysis. Moulting and epigenesis become desynchronized after the first few zoeal stages. This results in morphological variation in larvae with similar moulting histories (in terms of the number of moults), but in which epigenesis may have been proceeding at different rates. Also, the longer an intermoult period lasts so the next stage is more advanced. Superimposed on this is normal intraspecific variation including variation within a brood from one female.

The separate control of development and moulting is adaptive in that larvae are able to cope with sub-optimal conditions by slowing epigenetic development while continuing to moult. The animal is constrained physically by the rigid exoskeleton and moulting is essential to permit an increase in size. Epigenesis may be delayed, but moulting continues and may not always be accompanied by an increase in size. This results in so called 'repeat' moults (Rochanaburanon & Williamson, 1976; Fincham, 1977). As moulting uses up energy and increases vulnerability until the exoskeleton hardens after ecdysis, it is reasonable to assume that moulting has functions other than merely allowing an increase in size. It is not clear why moulting does not cease in poor conditions. It has been shown, from analysis of whole larvae, however, that organic substances including proteins and amino acids and inorganic ions such as K^+, Ca^{++}, Mg^{++} rise in concentration during premoult and decrease at postmoult, and the reverse occurs in concentrations for Na^+ and Cl^- (Torres, 1973; Charmantier, 1977). The periodic release into the haemolymph of these molecules and ions may be necessary to make them available for stages in the epigenetic sequence. This leads to the development of the new structures, which in the larval stages is continuous even if, in response to poor external environmental conditions, the rate is slow.

Meristic and morphological variation (Tables 1, 2)

In a study of morphological variation in natural populations of the smooth newt, Bell (1974) found that animals of average length survive in conditions of stress such as the critical period of metamorphosis. As the total length increases, therefore, so variation in this character would be expected to decrease. Waddington (1948) pointed out that development is canalized with a strong tendency for the adult to conform to the morphological norm within prescribed limits. In a later paper Waddington (1953) discussed the inflexibility of the biochemical pathways controlled by the epigenotype during development. These pathways lead inevitably to a similar end result, to a large extent regardless of unfavourable influences from the genotype or the environment. Bell (1974) stated that '. . . the epigenetic system is so constructed that individuals which are originally quite different tend to become more similar as their development proceeds'.

Both developmental canalization (stabilizing selection) and natural (normalizing) selection have the effect of reducing variation. Bell (1974), however, was able to eliminate the former in accounting for the decrease in variation in the two morphometric characters (standard length and head width) as the larvae approached metamorphosis. This was achieved by keeping laboratory populations of newt larvae in near optimum conditions. Overall survival was better than for equivalent wild populations since external natural selection was less intense in the laboratory, whereas the internal stabilizing selection would have been the same in both wild and laboratory populations. This reduction in variation of larval size distribution was reversed in post-metamorphosis newts and was corroborated by dentition data (Bell, 1975). The obvious advantage of such selective processes is that only typical representatives of the species survive metamorphosis.

The present morphometric results (Table 2) parallel the findings of Bell and show that there is a significant reduction ($P<0{\cdot}05$) in variation or normalizing selection of larval size as *Palaemonetes* (*Palaemonetes*) *varians* approached metamorphosis, with a tendency to increase in post-metamorphosis shrimps. All other correlations of meristic characters were not significant and there was no tendency for individuals to become more similar as suggested by Bell (1974). Particular attention was given to the shrimp mouthparts since Bell (1975) found newt dentition data corroborated his morphometric findings. To compare these results of *Palaemonetes* (*Palaemonetes*) *varians*, data (Fincham, 1977) from a closely related palaemonid *Palaemon* (*Palaeander*) *elegans* was analysed to test for changes in variation as metamorphosis approached. In the latter species even morphometric data were not significant. There was, however, a significant *increase* in variation of the plumose setae on the exopodite of mouthpart maxilla 2 in the pre-metamorphosis stages ($P<0{\cdot}01$). Clearly there is no simple, general correlation between larval variation and the approach of metamorphosis.

Some similarities in habitat exist between the newt and *Palaemonetes* (*Palaemonetes*) *varians*: both live in shallow ephemeral bodies of water and both showed a reduction in overall length variation. A rigorous selection process may be necessary to ensure survival in this particular habitat. The increase in variation of maxilla 2 in *P.* (*P.*) *elegans* – a genuine increase and not simply a corollary of increased size – presents a totally unexpected reversal of normalizing selection. This shrimp is a common inhabitant of intertidal rockpools and undergoes 6–9 zoeal moults before metamorphosis. The larvae are planktonic and have access to a wide variety of coastal habitats when they become benthic after the final larval stage. There is a degree of uncertainty in making immediate contact with the most suitable rocky coastline and a degree of variation would clearly be advantageous.

Gurney (1924) stated '. . . a knowledge of the larval history is of importance in tracing the systematic relationships of Decapoda . . .'. One of the aims of this present series of papers is to provide detailed descriptions of larval stages to aid identification and to form the basis of a systematic study using numerical methods. For this purpose the extent of larval variation needs to be determined. Gurney (1924) gave details of intermediate post larval stages in which various combinations of late larval and first post larval characters were found. While these were not unknown in the present study, rearing at 22 °C produced a rapid, and in most cases direct, development to PL1 through five larval stages. The delay in the epigenetic process recorded by Gurney was probably a response to environmental stress imposed by the rearing techniques. With regard to larval polymorphism or poecilogony (Boas, 1889; Heldt, 1953) abundant larval variation was recorded in the present study but this did not exceed variability commonly found in larval prawns and shrimps.

Acknowledgement

It is a pleasure to thank Peter Warren, MAFF Fisheries Laboratory, for introducing me to Burnham-on-Crouch ditches and Ann Gurney, BM(NH) Crustacea Section, for assisting ably with larval rearing.

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Manuscript accepted for publication 17 May, 1977

A revision of the spider genus *Brettus* (Araneae: Salticidae)

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Introduction

The genus *Brettus* was proposed by Thorell (1895) for the Burmese species *Brettus cingulatus* Thorell. Simon (1900) described four more species (*Brettus martini* from South Africa, *B. albolimbatus* and *B. semifimbriata* from India and *B. adonis* from Sri Lanka) and in 1901 synonymized the genus with *Portia*. Wanless (1978*b*) revised *Portia* and resurrected *Brettus* in part. *Brettus martini* Simon could not be recognized from the original description and as the type specimen could not be found the name was considered a *nomen dubium*. In the present paper the genus is redefined and its affinities discussed. The four known species (of which one is new) are described and keyed. One species is newly synonymized and three lectotypes designated.

The measurements were made in the manner described by Wanless (1978*a*).

The known species of *Brettus* are closely related and occur in the Oriental region. They resemble spiders of the genus *Portia*, but are generally smaller in size and lack the abdominal hair tufts. Unfortunately their biology is unknown though it is considered that their behaviour may be similar to that described for some species of *Portia* (Wanless, 1978*b*), and that specimens may be found living in diplurid or pholcid webs.

Genus *BRETTUS* Thorell

Brettus Thorell, 1895 : 354. Type species *Brettus cingulatus* Thorell, by original designation and monotypy. Simon, 1901 : 402 [=*Portia*] Petrunkevitch, 1928 : 213. Bonnet, 1955 : 915. Wanless, 1978*b* : 84 [gen. rev.].

Definition. Small to medium spiders ranging from about 3·0 to 8·0 mm in length. Sexes alike; leg fringes present, but abdominal hair tufts apparently lacking; colour patterns composed of setae (easily rubbed). *Carapace*: high, longer than broad; fovea present, behind posterior lateral eyes; sculpturing not marked, cuticle weakly iridescent (under some angles of illumination); in most species, broad marginal bands composed of white setae extend from clypeal region to posterior thoracic margin. *Eyes*: anteriors subcontiguous with apices recurved; posterior median eyes relatively large, nearer to anterior laterals than to posterior laterals; posterior row narrower than anterior row; quadrangle length between 40 and 50 per cent of carapace length. *Clypeus*: moderately high to high, concave. *Chelicerae*: medium to large, more or less vertical; promargin with 3 teeth, retromargin with 3 to 4. *Maxillae*: elongate, usually divergent. *Labium*: subtriangular, about half maxilla length. *Sternum*: elongate scutiform. *Pedicel*: short. *Abdomen*: elongate ovoid; scuta lacking, but four impressed spots usually present; anterior and posterior spinnerets robust, subequal in length, medians slender, relatively short; trachea not examined (insufficient material). *Legs*: long and slender, fringes present on legs I and sometimes II; spines numerous, moderately robust; claws pectinate, tufts present, scopula lacking; legs I–II with minute setae in parallel row on venter of tarsi and metatarsi. *Female palp*: long and slender with terminal claw (difficult to see). *Male palp*: femoral apophyses lacking; tibiae with lateral and ventral apophyses, the former with an associated duct which appears to arise from a flask-like vacuole (Fig. 1E, F). Cymbium modified proximally; embolus very long and slender; conductor apparently lacking; tegulum with peripheral seminal reservoir, a curved furrow (Fig. 1A, B) and a bipartite membraneous apophysis (apparently lacking in *B. adonis*) adjacent to the embolic base; median

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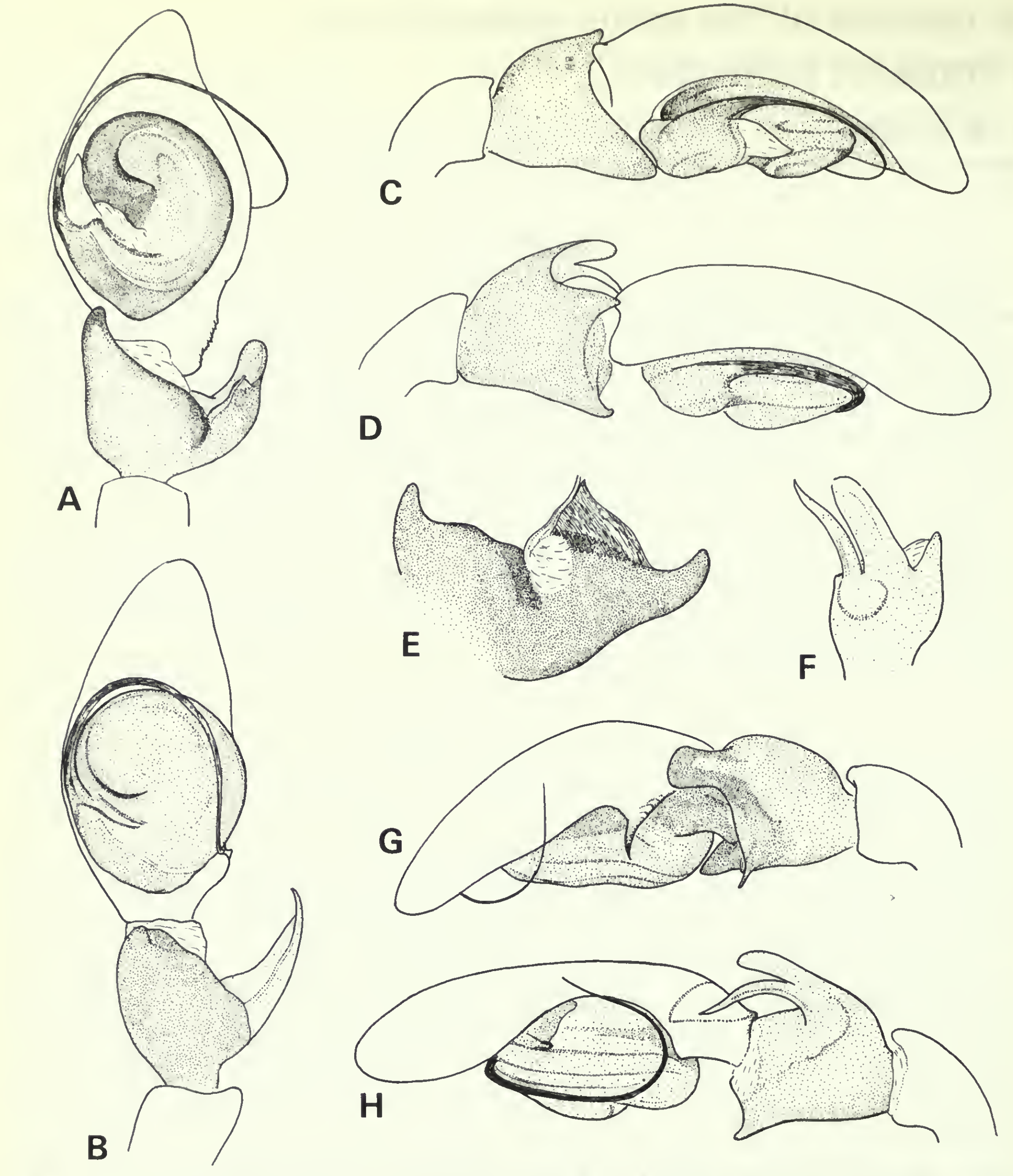

Fig. 1 (A, C, E, G) *Brettus cingulatus* Thorell, holotype ♂: (A) palp, ventral view; (C) palp, mesal view; (E) palpal tibia, posterior view; (G) palp, ectal view. (B, D, F, H) *B. adonis* Simon, ♂: (B) palp, ventral view; (D) palp, mesal view; (F) palpal tibia, dorsolateral view; (H) palp, ectal view.

apophysis lacking. *Epigyne*: relatively simple; openings usually indistinct, leading to elongate ducts which terminate distally as spermathecae.

AFFINITIES. Wanless (1978*b*) suggested that on behavioural and anatomical grounds *Portia*, *Brettus*, *Cocalus* and several other genera with large posterior median eyes could be related to lyssomanid spiders and that *Brettus* may form a link between *Portia* in the Salticidae and *Asemonea* in the Lyssomanidae. Unfortunately the link cannot be satisfactorily demonstrated from the known species of *Brettus* which are evidently closer to *Portia* than to *Asemonea*. Preliminary observations on male *Asemonea* have shown that the palps are generally very complex and that some males (e.g. *A. tenuipes* O.P.-C.) apparently have ducts associated with the femoral apophyses. The presence of these ducts may indicate a distant relationship with *Brettus*, but their significance cannot be evaluated at the present time.

DIAGNOSIS. *Brettus* is distinguished from *Portia* by the very long embolus and the apophysal duct on the tibiae in males, and the long fertilization ducts in females. A fuller diagnosis cannot be given until other related genera have been revised.

List of species in the genus *Brettus* Thorell, 1895

Brettus adonis Simon, 1900
B. albolimbatus Simon, 1900
B. anchorum sp. n.
B. cingulatus Thorell, 1895

Key to speices of *Brettus*

1 Males – 2
– Females 3
2 Retrolateral tibial apophysis not bifurcate, ectal margin of cymbium with pointed spur (Fig. 1G) (Burma) . . . . ***cingulatus*** Thorell (p. 185)
– Retrolateral tibial apophysis bifurcate, ectal margin of cymbium lacking pointed spur (Fig. 1H) (Sri Lanka) . . . . ***adonis*** Simon (p. 186)
3 Distal margin of epigynal plate clearly projecting beyond epigastric fold (Fig. 3A) (Sri Lanka) ***adonis*** Simon (p. 186)
– Distal margin of epigynal plate not projecting beyond epigastric fold 4
4 Spermathecae extending laterally (Figs 3B; 4C, D) (India) . . ***anchorum*** sp. n. (p. 188)
– Spermathecae extending anteriorly (Figs 3C, D; 4A, B) (India) . . ***albolimbatus*** Simon (p. 188)

Brettus cingulatus Thorell

(Figs 1A, C, E, G; 2A, B)

Brettus cingulatus Thorell, 1895 : 355, ♂. Holotype ♂, Burma, Tharrawaddy (NR, Stockholm, no. 1605) [Examined]. Wanless, 1978*b* : 83.

Portia cingulata: Simon, 1901 : 402. Reimoser, 1925 : 90. Roewer, 1954 : 934. Bonnet, 1958 : 3766. Prószyński, 1971 : 461.

DIAGNOSIS. The male of *B. cingulatus* is readily distinguished from that of *Brettus adonis* by the pointed spur on the ectal margin of the cymbium (Fig. 1G).

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 2A, B): orange-brown with paler eye region and a wide marginal band composed of recumbent, silky white hairs from clypeus to posterior thoracic margin. *Eyes*: with black surrounds except AM; anteriors fringed by whitish hairs. *Clypeus*: densely clothed in silky white hairs. *Chelicerae*: orange-brown; thinly covered in fine light brown hairs; promargin with 3 teeth, retromargin with 4. *Maxillae and labium*: pale orange-brown tinged with grey. *Sternum*: light orange-brown with poorly defined reddish orange margins; sparsely clothed in dull white hairs. *Abdomen*: rubbed; light yellow-orange tinged with black; pattern indistinct. *Legs*: anteriors dark orange-brown, posteriors lighter; brown ventral fringes present on femora, patellae and tibiae of legs I and II; spines numerous, moderately robust. *Palp* (Fig. 1A, C, E, G).

Dimensions (mm): total length 5·6; carapace length 2·56, breadth 2·2, height 1·48; abdomen length 2·88; eyes anterior row 1·44, middle row 1·08, posterior row 1·28; quadrangle length 1·08. *Ratios*: AM : AL : PM : PL : 12·5 : 6·5 : 5 : 6; AL–PM–PL : 6·5–9.

DISTRIBUTION. Burma.

MATERIAL EXAMINED. Holotype ♂, data given in synonymy.

Brettus adonis Simon comb. rev.

(Figs 1B, D, F, H; 2D, E; 3A)

Brettus adonis Simon, 1900 : 32, ♀, Lectotype ♀ (here designated) Sri Lanka, Galle (MNHN, Paris, no. 20416) [Examined].

Portia adonis (Simon): Simon, 1901 : 402. Roewer, 1954 : 934. Bonnet, 1958 : 3766. Prószyński, 1971 : 461.

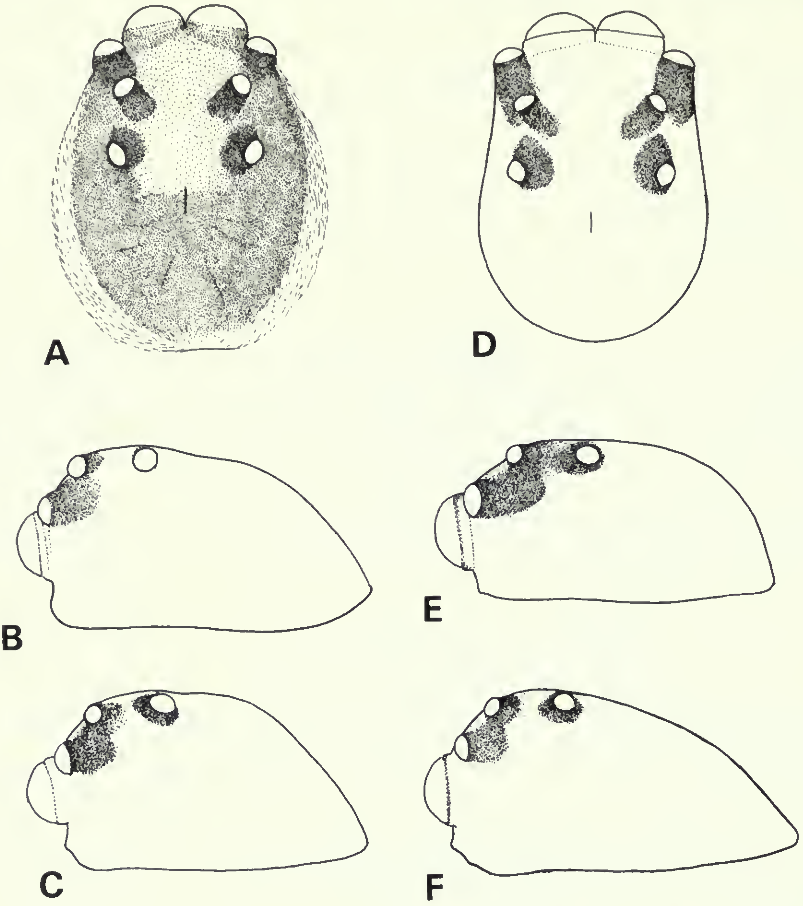

Fig. 2 (A, B) *Brettus cingulatus* Thorell, holotype ♂: (A) carapace, dorsal view; (B) carapace, lateral view. *B. albolimbatus* Simon, lectotype ♀: (C) carapace, lateral view. (D, E) *B. adonis* Simon, ♂: (D) carapace, dorsal view; (E) carapace, lateral view. *B. anchorum* sp. n. holotype ♀: (F) carapace, lateral view.

The vial labelled '20416 Port Adonis [sic] E. S. Galle type' contains one male and one female. The female is considered to be the type specimen and is designated lectotype. The male, which appears to be conspecific, is described below.

Diagnosis. *B. adonis* is distinguished from *Brettus cingulatus* by the absence of a pointed spur on the ectal margin of the cymbium in males (Fig. 1H), and the posterior projection of the epigynal plate in females (Fig. 3A).

Male from Galle, Sri Lanka. *Carapace* (Fig. 2D, E): light orange with yellow-orange eye region; very sparsely clothed in minute iridescent setae (mostly rubbed). *Eyes*: with black surrounds except AM; anteriors fringed by pale yellow hairs. *Clypeus*: fringed by short silky white hairs. *Chelicerae*: yellow with faint sooty markings; fringed proximally with transverse band of silky white hairs; teeth not examined. *Maxillae and labium*: yellow tinged with grey. *Sternum*: yellow, glossy. *Abdomen*: yellow with faint blackish mottling; very sparsely clothed in minute iridescent setae. *Legs*: legs I orange to pale orange, lightly tinged with black; remaining legs pale yellow; legs I densely fringed by stiff orange-brown hairs on venter and dorsum of tibiae, venter of patellae and distal venter of femora. Spines moderately robust and numerous. *Palp* (Fig. 1B, D, F, H).

Dimensions (mm): total length 3·16; carapace length 1·65, breadth 1·28, height 0·92; abdomen length 1·44; eyes anterior row 1·08, middle row 0·84, posterior row 0·92; quadrangle length 0·80. *Ratios*: AM : AL : PM : PL : 9·5 : 4·5 : 3·5 : 4; AL–PM–PL : 5–6·5.

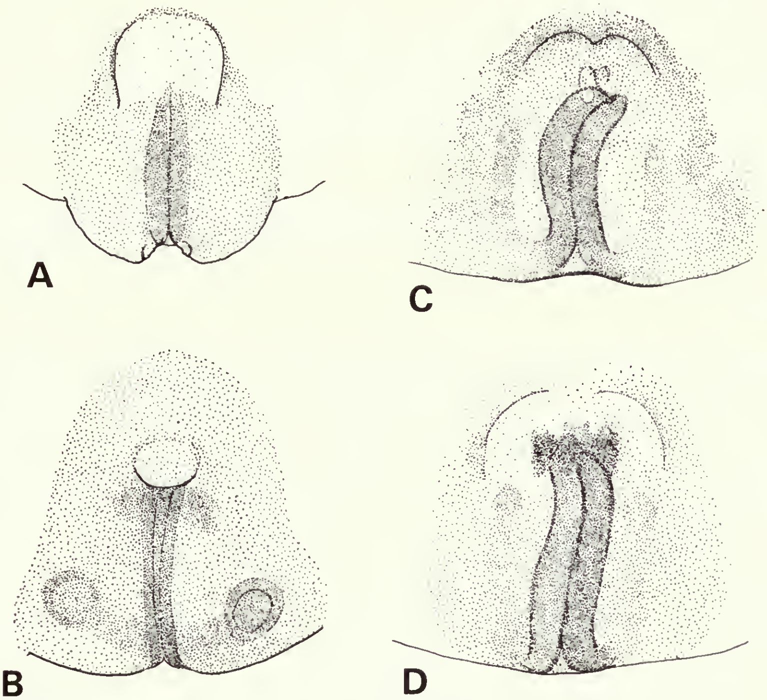

Fig. 3 *Brettus adonis* Simon, lectotype ♀: (A) epigyne. *B. anchorum* sp. n. holotype ♀: (B) epigyne. (C, D) *B. albolimbatus* Simon, lectotype ♀: (C) epigyne; paralectotype ♀: (D) epigyne.

Female lectotype. Body form and colour similar to ♂. *Carapace*: as in ♂, but irregularly clothed with recumbent white hairs, iridescent under some angles of illumination, apparently forming a wide marginal band from clypeus to posterior thoracic margin. *Eyes*: more or less as in ♂. *Clypeus*: thinly clothed in fine whitish hairs. *Maxillae and labium*: as in ♂. *Sternum*: as in ♂. *Abdomen*: pale yellow with a greyish tip and markings forming an ill-defined ventral band from spinnerets to epigyne. *Legs*: similar to ♂ but dorsal fringes on legs I lacking and with patellae and ventral tibial fringes composed of long white hairs proximally. *Palps*: long and slender, whitish yellow with white hairs. *Epigyne* (Fig. 3A): vulva not examined.

Dimensions (mm): total length 4·6; carapace length 1·96, breadth 1·56, height 1·04; abdomen length 2·52; eyes anterior row 1·27, middle row 0·98, posterior row 1·12; quadrangle length 0·96. *Ratios*: AM : AL : PM : PL : 11·5 : 6 : 4 : 5; AL–PM–PL : 6–8.

Distribution. Sri Lanka.

Material examined. Lectotype ♀, data given in synonymy. Sri Lanka: Galle, 1 ♂ in the same vial as the lectotype.

Brettus albolimbatus Simon comb. rev.

(Figs 2C; 3C, D; 4A, B)

Brettus albolimbatus Simon, 1900 : 31, ♀. LECTOTYPE ♀ (here designated) India, Trichinopoly (MNHN, Paris, no. 17534) [Examined].

Portia albolimbata (Simon): Simon, 1901 : 402. Roewer, 1954 : 934. Bonnet, 1958 : 3766. Prószyński, 1971 : 461. Wanless, 1978*b* : 85.

Brettus semifimbriatus Simon, 1900 : 31, ♀. LECTOTYPE ♀ (here designated) India, Trichinopoly (MNHN, Paris, no. 18918) [Examined]. **Syn. n.**

Portia semifimbriata (Simon): Simon, 1901 : 401, 402. Strand, 1912 : 148. Roewer, 1954 : 934. Bonnet, 1958 : 3767. Wanless, 1978*b* : 85.

Portia foveata Strand, 1912 : 148. [Published as a synonym of *P. semifimbriata* (Simon).]

The vial labelled '17534 Port. Scultzi Karch [sic] (albolimbata E. S. type) Natal C.M.' contains one female which is conspecific with the lectotype of *Brettus semifimbriatus* Simon. In view of this conspecificity and the reference to 'albolimbata E. S. type' on the label, the locality and collector data, i.e. Natal, C[h]. M[artin], is probably erroneus and the specimen is considered to be the type of *B. albolimbata*.

DIAGNOSIS. *B. albolimbatus*, known only from the female, is distinguished from other females of *Brettus* by the S-shaped fertilization ducts and the anteriorly extended spermathecae (Figs 3C, D; 4A, B).

MALE. Unknown.

FEMALE LECTOTYPE. *Carapace* (Fig. 2C): light orange-brown with yellow-orange eye region and faint sooty marking radiating from fovea; shiny and weakly iridescent under some angles of illumination; from AL to posterior thoracic margin a broad white marginal band composed of recumbent white hairs. *Eyes*: with black surrounds except AM; anteriors fringed by whitish hairs. *Clypeus*: thinly covered in white hairs. *Chelicerae*: pale orange-brown with sooty markings; sparsely clothed in long fine pale orange hairs; pro- and retromargins with 3 teeth. *Maxillae and labium*: light orange-brown tinged with grey. *Sternum*: light orange-brown, shiny; thinly clothed in fine light orange hairs. *Abdomen*: whitish yellow tipped with grey, with greyish markings dorsally and subparallel bands from epigyne to spinnerets; irregularly clothed in white and orange-brown hairs (rubbed). *Legs*: pale yellow to orange-brown with ventral brown fringes on tibiae I, patellae I and femora I; similar fringes on legs II, but less dense; spines numerous, moderately robust. *Palp*: white with yellowish tips. *Epigyne* (Fig. 3C).

Dimensions (mm): total length 5·04; carapace length 2·4, breadth 2·0, height 1·4; abdomen length 2·76; eyes anterior row 1·44, middle row 1·14, posterior row 1·26; quadrangle length 0·98. *Ratios*: AM : AL : PM : PL : 12·5 : 6 : 5 : 5·5; AL–PM–PL : 7–9.

VARIATION. Females vary from 5·04 to 7·2 mm total length, 2·4 to 2·9 mm carapace length (three specimens). The appearance of the epigynal fertilization ducts is evidently variable (Fig. 3C, D).

DISTRIBUTION. India.

MATERIAL EXAMINED. Lectotype females, data given in synonymy. INDIA: Madras, Trichinopoly, 1 ♀ paralectotype in the same vial as the lectotype of *B. semifimbriatus* (no. 18918).

Brettus anchorum sp. n.

(Figs 3B; 4C, D)

DIAGNOSIS. *B. anchorum*, known only from the female is separated from other females of *Brettus* by the laterally extended spermathecae (Figs 3B; 4C, D).

MALE. Unknown.

FEMALE HOLOTYPE. *Carapace* (Fig. 2F): pale orange with yellowish eye region and broad marginal bands of recumbent white hairs from AM to posterior thoracic margin. *Eyes*: with black surrounds except AM; anteriors fringed by white hairs. *Clypeus*: thinly clothed in whitish hairs. *Chelicerae*: pale orange with long fine white hairs; promargin with 3 teeth, retromargin with 4. *Maxillae and labium*: pale orange tinged with grey. *Sternum*: light yellow, shiny. *Abdomen*: whitish yellow. *Legs*: whitish yellow to orange; tibiae I, patellae I and distal half of femora I ventrally fringed by stiff orange-brown hairs. *Palp*: light yellow. *Epigyne* (Figs 3B; 4C, D).

Dimensions (mm): total length 7·82; carapace length 2·72, breadth 2·36, height 1·48; abdomen length 4·7; eyes anterior row 1·4, middle row 1·08, posterior row 1·26; quadrangle length 1·12. *Ratios*: AM : AL : PM : PL : 13 : 6 : 5 : 6; AL–PM–PL : 7–9·5.

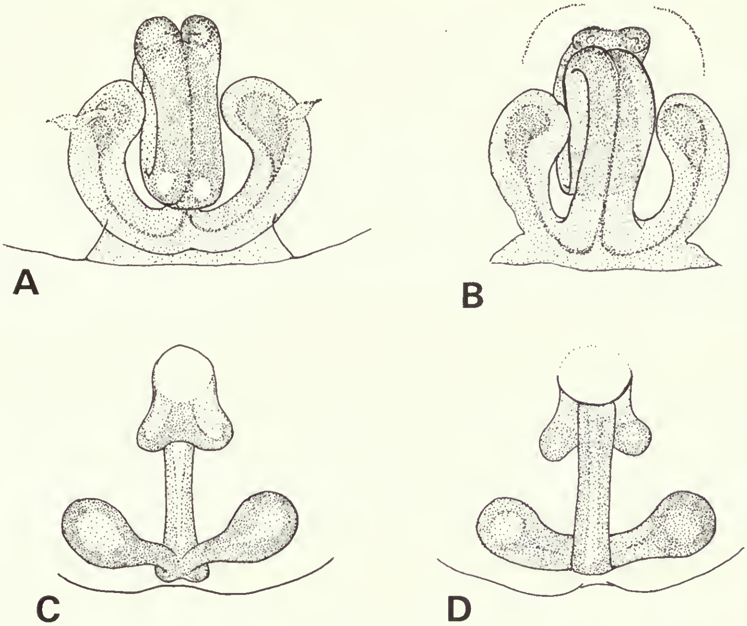

Fig. 4 (A, B) *Brettus albolimbatus* Simon, paralectotype ♀: (A) vulva, ventral view; (B) vulva, dorsal view. (C, D) *B. anchorum* sp. n. holotype ♀: (C) vulva, ventral view; (D) vulva, dorsal view.

Distribution. India.

Material examined. Holotype ♀, India, Madras, Nilghiri Hills (*Sir George Hampson*) (BMNH. Reg. No. 1977.12.21.1).

Acknowledgements

I wish to thank the following colleagues for providing specimens for study. M. M. Hubert, Muséum national d'Histoire naturelle, Paris, France (MNHN, Paris) and Professor T. Kronestedt, Naturhistoriska Riksmuseet, Stockholm, Sweden (NR, Stockholm).

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Manuscript accepted for publication 10 November, 1977

Notes on the osteology of the Arab horse with reference to a skeleton collected in Egypt by Sir Flinders Petrie

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Synopsis

A horse skeleton from Egypt donated by Sir Flinders Petrie to the British Museum (Natural History) and previously assumed to be ancient has been shown by radiocarbon dating to be only about three to four hundred years old. As a result of this, the skeleton has acquired an altogether different importance as a rare source of comparative material relevant to the history and development of the Arab horse. Comparative measurements of the skeletons of two modern Arab horses show that these closely resemble the Petrie horse. Other valuable osteological material collected by Petrie is briefly discussed.

Introduction

Amongst the material in the osteology collections of the Mammal Section at the British Museum (Natural History) is the skeleton of a horse donated by Sir Flinders Petrie, probably at the beginning of this century. There is no documentation with the skeleton to give its historical age, date of collection or provenance beyond the fact of its having come from Egypt. The skeleton has recently been registered in the Museum's computer catalogue of archaeological animal remains as ARC 1977 5101.

The earliest evidence for the domestic horse in Ancient Egypt is at present the single skeleton from the Middle Kingdom fortress of Buhen in northern Sudan, dated historically to *circa* 1675 B.C. (Clutton-Brock, 1974), and there are in fact very few remains of horses even from later periods in Egypt. For this reason and because the Petrie skeleton is remarkably complete, except for the cranial region which is unfortunately fragmentary, we were anxious to establish its date and locality. The age could be determined by radiocarbon dating, but the locality has proved more elusive.

There appears to be no mention of the horse skeleton in any publication by Petrie, and we have examined all the relevant manuscripts and other records held by the Egypt Exploration Society and in the Petrie Museum of the Department of Egyptology at University College London. The documents in the Petrie Museum have been recently catalogued by Mrs Barbara Adams (1975, pp. 108–111) and include photocopies of original journals held at the Griffith Institute, Ashmolean Museum, Oxford, the other main repository of the Petrie archives. Unfortunately, we found no reference to the horse skeleton although there were several useful references to other animal remains held at the British Museum (Natural History).

Despite the absence of records we considered it justifiable to proceed with the radiocarbon dating in the hope that it would shed light on the early history of the horse in Egypt. To our initial dismay this date came out at only 328 radiocarbon years before the present, that is to the early seventeenth century A.D.

It took a little time to overcome our surprise at this result, and to become reconciled to the fact that we were no longer dealing with a specimen from Ancient Egypt, but we then realized that the skeleton has considerable intrinsic value. This is we believe the only well-dated skeleton

Bull. Br. Mus. nat. Hist. (Zool.) **35** (2): 127–200 Issued 26 April, 1979

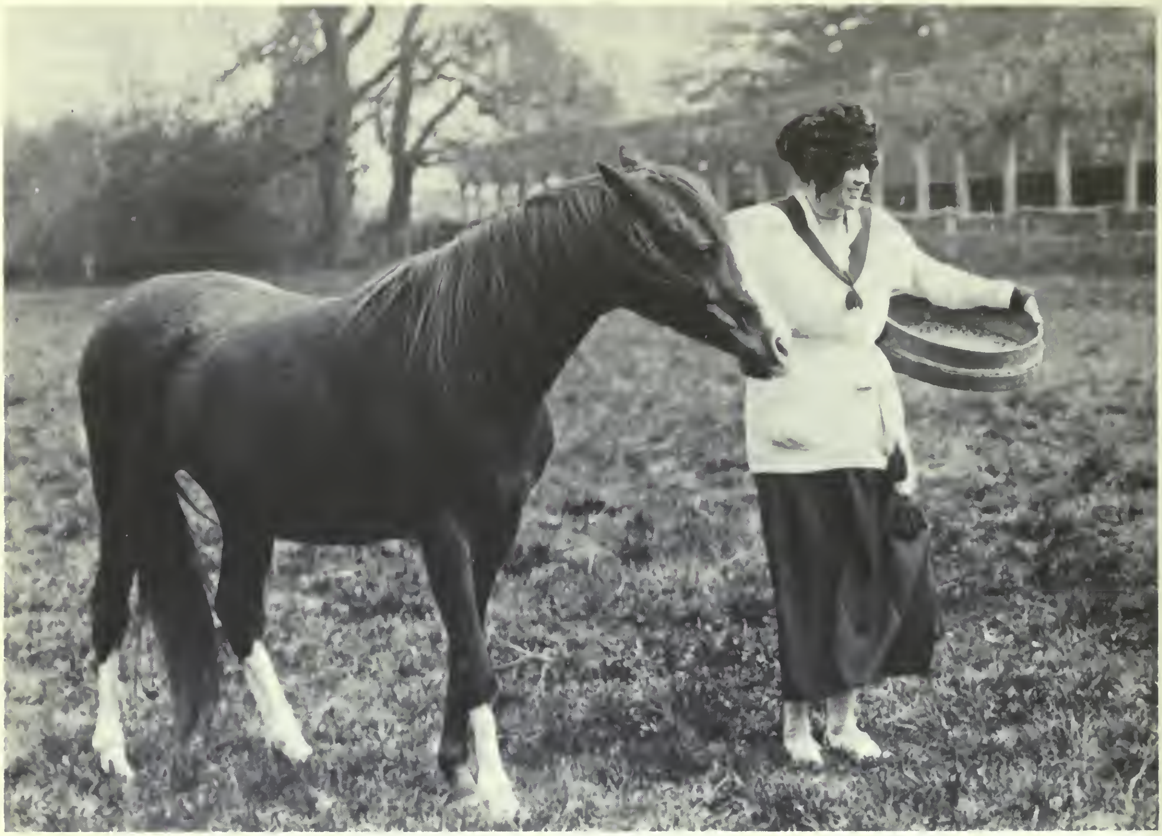

Fig. 1 The Arab mare Ajjam with Lady Wentworth. (Photo: Special Press.)

of a horse that comes from the North African region, at a period when horses were beginning to undergo intensive improvement in Britain by cross-breeding with stock imported from the East. To anyone interested in the history of the Arab horse this skeleton should therefore be of value as comparative material, for it was in about A.D. 1689 that the first of the famous Arabs, Byerley Turk, arrived in England. As far as is known, there are no extant remains of the original imported Arab horses so we have not been able to make direct metrical comparisons with contemporary skeletons. However, detailed measurements have been recorded of the Petrie horse and compared with two Arab skeletons from the modern collections of the British Museum (Natural History) (Tables 1 and 2). One of these skeletons, No. 37.1.26.9, is of Ajjam, an Arab mare that died in 1937. Ajjam was owned by Lady Wentworth, who as is well known, was the daughter of Lady Anne Blunt, and had a world-famous stud of imported Arab stock at Crabbet Park in Sussex (Fig. 1).

We cannot be certain, of course, that the skeleton of the horse collected by Petrie in Egypt was of Arab breed, but it can be seen from the measurements that the bones bear a close resemblance to the two modern Arab skeletons.

Osteological description

The skeleton of the seventeenth century A.D. horse that was presented to the British Museum (Natural History) by Sir Flinders Petrie, was from an aged animal that was certainly more than 20 years old at the time of death, and may have been more than 30 years. The age was assessed from the state of wear on the upper left corner and intermediate incisors (I^2 and I^3), these being the only incisor teeth present.

The skull and upper jaws of the horse only remain as comminuted fragments, but there is enough of the diastema region of the left maxilla and premaxilla to indicate that no canine tooth was present. There is therefore a high probability that the animal was female and this assertion is supported by the shape and proportions of the pelvic bones. The post-cranial bones are almost all present and are well enough preserved to enable measurements to be taken on each bone from either the left or right side of the skeleton. These measurements which were taken according to the method of von den Driesch (1976), are given in Table 1, whilst the dimensions of the lower cheek teeth are given separately in Table 2. Although most of the bones were complete, their condition was fragile so it was decided to impregnate them with polyvinyl acetate (PVA emulsion) to conserve them. This was carried out on the whole skeleton with the exception of the left humerus, some ribs and the right ulna which was destroyed for the radiocarbon determination.

When choosing modern comparative material to be measured against the Petrie horse we decided to take the skeleton of the Arab mare Ajjam (BM(NH) No. 37.1.26.9), although its skull was not available for measurement, and it was immediately apparent that the bones of the two specimens were very similar in their proportions. In addition an Arab stallion, Little Joker (BM(NH) No. H.40, presented by the Bombay Veterinary College in 1911), was selected for measurement and in this specimen the skull is complete so its gross dimensions are included in Table 1. The skull of the Petrie horse is unfortunately too fragmentary to allow any valid measurements to be recorded from it, but the mandible is complete except for the incisor region, so this may be compared with the mandible of the stallion, Little Joker. It can be seen that the lower teeth of the Petrie mare are considerably smaller than those of the stallion, but this is at least partly due to the greater age of the mare when it died and consequently the heavier wear on its cheek teeth. Although these teeth are much worn they are healthy and show no unevenness from biting on a bit.

The Petrie skeleton is from a large horse; it stood more than 15 hands (1509 mm) at the withers when it was alive (Table 1) and this is high, especially for a mare. The bones show that the animal was fine-limbed, and although it is not possible to tell the breed from an examination of the skeleton the proportions are close to those of the modern Arab mare and stallion that were taken as comparative material. The slenderness index of the metacarpal (Table 1) indicates that the Petrie mare was slightly more stockily built than the mare Ajjam, but only marginally more so than the stallion Little Joker, and in overall height she was taller than the stallion.

The numbers of vertebrae in the Petrie skeleton and the two comparative skeletons are as follows:

	Petrie mare	*Ajjam*	*Little Joker*
Cervical	7	7	7
Thoracic	18	18	17
Lumbar	5 (estimated)	5	6

The fifth lumbar vertebra is missing in the Petrie skeleton but it is evident from examination of the articular surfaces of the fourth lumbar and the sacrum that this mare only had five lumbar vertebrae. Stecher (1962) carried out a numerical survey of the numbers of vertebrae in the spines of modern horses, and he provided authoritative support for the contention of horsemen that the purebred Arab horse is ‘short-coupled’, that is, compared to other races of horses, it has a reduced number of vertebrae. Stecher found that the more usual number of six lumbar vertebrae was often reduced to five in Arab horses, and that if six lumbars were present then the thoracic vertebrae were reduced from the more usual 18 to 17. The two skeletons of Ajjam and Little Joker provide examples of these two alternative numberings, whilst that of the Petrie mare is consistent with the usual number found in the Arab breed.

In both Ajjam and Little Joker the two posterior lumbar vertebrae are fully ankylosed, indicating that both these horses were ridden extensively before they were fully mature. Although the Petrie mare was an aged animal when it died, there is no sign of ankylosis or other pathological condition in the spine which appears to be perfectly healthy. The rest of the skeleton of the Petrie

Table 1 Measurements of the Petrie horse skeleton together with those from male and female modern Arab horse skeletons. All measurements are in mm. Figures in brackets are estimates

	Designation as in von den Driesch (1976)	Petrie horse 77.5101 ♀	Ajjam 37.1.26.9 ♀	Little Joker H.40 ♂
Skull				
Basal length	**3**	–	–	482·0
Condylobasal length	**2**	–	–	510·0
Brow width (max.)	**41**	–	–	192·3
Breadth of cranium	**38**	–	–	99·0
Max. width occ. condyles	**34**	–	–	87·9
Max. A-P diameter of orbit	**31**	–	–	57·7
Max. D-V diameter of orbit	**32**	–	–	55·2
Mandible				
Length	**1**	–	–	386·2
Width of condyle	**–**	47·5	–	53·9
Depth of ramus between M_2–M_3	**–**	–	–	80·0
Height of vertical ramus	**19**	220·0	–	216·3
Atlas				
Max. width	GB	(140·3)	142·0	151·0
Axis				
Max. width of articular surface (ant.)	BFcr	86·1	87·6	91·5
Min. width of vertebra	SBV	43·6	48·5	52·7
Scapula				
Min. width of neck	SLC	67·3	66·7	66·1
Length of glenoid cavity	LG	58·0	62·0	64·0
Width of glenoid cavity	BG	44·0	51·2	49·4
Length of glenoid cavity + coronoid process	GLP	97·1	95·8	97·8
Height	HS	350·0	352·0	328·0
Humerus				
Length	GL	(310·0)	314·0	304·0
Lateral length	GLl	(310·0)	314·0	304·0
Distal width	BT	77·4	81·2	83·0
Radius				
Length	GL	358·0	368·0	351·0
Lateral length	GLl	351·0	350·0	337·0
Proximal width	BFp	76·3	80·4	81·4
Distal width	BFd	64·8	67·1	68·8
Min. width of shaft	SD	39·0	40·4	39·0
Ulna				
Length of head	LO	83·8	82·0	81·5
Width of articular surface	BPC	43·6	47·9	48·7
Metacarpal				
Length	GL	242·1	251·5	240·0
Lateral length	GLl	240·0	247·0	236·6
Proximal width	Bp	49·6	53·5	54·2
Distal width	Bd	53·1	50·3	53·7
Min. width of shaft	SD	33·9	32·3	32·3

Table 1 (*cont.*)

	Designation as in von den Driesch (1976)	Petrie horse 77.5101 ♀	Ajjam 37.1.26.9 ♀	Little Joker H.40 ♂
Pelvis				
Max. length of innominate bone	GL	(405·0)	445·0	410·0
Length of acetabulum	LAR	62·4	67·6	66·9
Femur				
Length	GL	(420·0)	436·0	411·0
Lateral length	GLl	(420·0)	436·0	411·0
Proximal width	Bp	(116·0)	127·2	126·9
Distal width	Bd	–	97·4	98·9
Min. width of shaft	SD	41·2	41·8	38·8
Tibia				
Length	GL	389·0	390·0	368·0
Lateral length	GLl	360·0	355·0	335·0
Proximal width	Bp	96·4	101·8	102·6
Distal width	Bd	76·3	76·7	80·2
Min. width of shaft	SD	41·9	40·7	40·1
Talus				
Length	GH	62·7	62·6	64·0
Greatest width	GB	62·3	65·7	65·0
Calcaneum				
Max. length	GL	118·0	118·7	114·7
Phalanx I Fore				
Length	GL	93·9	93·2	90·4
Proximal width	Bp	56·3	54·6	58·0
Proximal depth	Dp	38·4	37·4	37·3
Distal width	Bd	46·3	46·4	49·6
Min. width of shaft	SD	34·2	34·3	35·0
Phalanx I Hind				
Length	GL	90·5	88·3	88·9
Proximal width	Bp	56·0	56·6	57·2
Proximal depth	Dp	41·6	40·2	40·4
Distal width	Bd	42·2	45·2	46·0
Min. width of shaft	SD	32·2	33·4	33·4
Phalanx II Fore				
Length	GL	49·4	44·5	49·0
Proximal width	Bp	54·2	52·9	54·5
Proximal depth	Dp	32·1	31·3	32·4
Phalanx II Hind				
Length	GL	51·4	46·9	50·0
Proximal width	Bp	53·6	52·5	54·9
Proximal depth	Dp	34·2	32·6	33·3

Table 1 (*cont.*)

	Designation as in von den Driesch (1976)	Petrie horse 77.5101 ♀	Ajjam 37.1.26.9 ♀	Little Joker H.40 ♂
Phalanx III Fore				
Length	GL	(60·9)	67·5	74·8
Width	GB	(83·7)	74·1	79·3
Height in region of extensor process	HP	(41·7)	47·8	36·6
Phalanx III Hind				
Length	GL	68·9	62·9	66·1
Width	GB	72·8	71·0	75·3
Height in region of extensor process	HP	47·7	45·8	38·0
Metatarsal				
Length	GL	288·3	300·0	288·5
Lateral length	GLl	285·4	295·0	282·3
Proximal width	Bp	53·5	55·3	55·0
Distal width	Dp	50·3	51·0	53·7
Min. width of shaft	SD	31·2	30·6	28·8
Sacrum				
Max. width of wings	GB	230·7	226·0	200·0
Length of body of sacrum without first caudal vertebra	PL	206·4	194·2	179·0
Slenderness index of metacarpal				
Min. width of shaft × 100/length	–	14·00	12·84	13·45
Estimate of withers height:				
Humerus				
Lateral length × 4·87	–	1509·7	1529·2	1480·5
Metacarpal				
Lateral length × 6·41	–	1538·4	1583·3	1516·6

Note: In Britain the withers height of living horses is usually measured by 'hands'. One hand = 101·6 mm.

mare is also healthy with the exception of the extensive exostoses on the mandible, described in the appendix below (see also Figs 2 and 3). Moreover, the hoof cores and anterior phalanges show no signs of the animal having been ridden or driven over hard ground, as is usual in aged horses that have been kept in primitive conditions and overworked.

As we have not been able to discover, up to now, how this mare came to be buried nor why it was later excavated by Sir Flinders Petrie and brought to England we can only speculate on its origins, but at least the healthy condition of the spine and limb bones does indicate that it was unlikely to have been a common beast of burden. One further small piece of evidence on its demise is provided by the tufa-like matrix that surrounded the fragments of skull. This is almost entirely composed of the casts of great numbers of fly larvae and pupae which have been identified by Mr K. G. V. Smith of the Department of Entomology, British Museum (Natural History) as belonging to *Chrysomya albiceps* (Wiedemann). This fly is found all over Africa and is a common feeder on carrion which means that the head of the mare must have been exposed to the open air, shortly after death, for long enough to become a breeding ground for flies that were later sealed in with sand or silt.

Table 2 Measurements of the lower teeth of the Petrie horse compared with the modern Arab male, H.40

	Designation as in von den Driesch (1976)	Petrie horse 77.5101 ♀	Little Joker H.40 ♂
Lower teeth			
Length of cheek teeth row	6a	160·0	162·2
Length of premolar row	8a	76·5	86·6
Length of molar row	7a	77·7	78·3
Length P_2	L	(28·0)	33·8
Width P_2	B	17·2	18·6
Length P_3	L	24·8	27·5
Width P_3	B	16·3	22·2
Length P_4	L	24·3	25·9
Width P_4	B	17·2	20·8
Length M_1	L	22·7	24·0
Width M_1	B	18·1	19·1
Length M_2	L	24·3	24·3
Width M_2	B	16·5	16·6
Length M_3	L	32·0	31.0
Width M_3	B	13·3	15·3

Dating

As mentioned above the right ulna of the horse was sacrificed to provide a sample for radiocarbon dating. The most reliable part of bone for radiocarbon dating purposes is collagen, the protein constituent, as dates on whole bones almost invariably prove to be too young. For this reason the olecranon process of the right ulna was first completely demineralized with dilute hydrochloric acid. A quantity of well-preserved, uncontaminated collagen was obtained which was converted chemically to benzene for measurement of ^{14}C activity by the liquid scintillation counting method. From this measurement the following date was obtained:

BM-1357. 328 ± 52 bp (ad 1622)

This result is expressed in radiocarbon years before A.D. 1950 on the basis of the 5570 year half-life, the normal mode of reporting dates at present. Thus the bp/ad notation indicates that this date has not been corrected for the known differences between radiocarbon and calendar years. These differences are not large in the period in which the date falls but the true calendar date to which it is approximately equivalent will be some 80 years earlier, that is about A.D. 1540. This corrected date has in turn an estimated error of about ±75 years at the level of one standard deviation.

Discussion

Although we do not know the reasons for the recovery of the skeleton of the horse or whether or not Petrie believed that it was ancient, it is not altogether surprising that he apparently kept no record. By comparison with the splendour and interest of the objects that Petrie uncovered in the

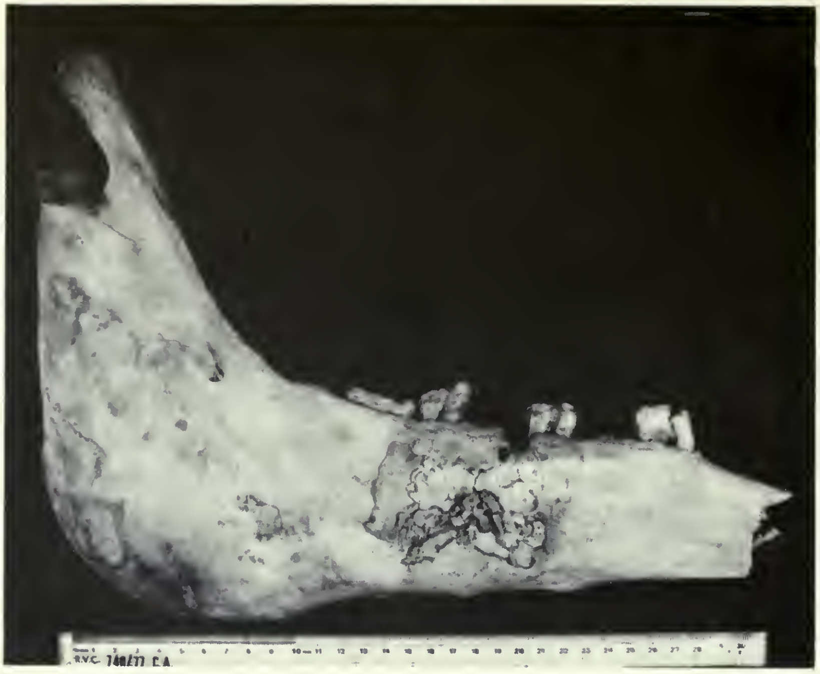

Fig. 2 Lingual side of left mandibular ramus of the Petrie horse showing extent of exostosis. (Photo: Royal Veterinary College.)

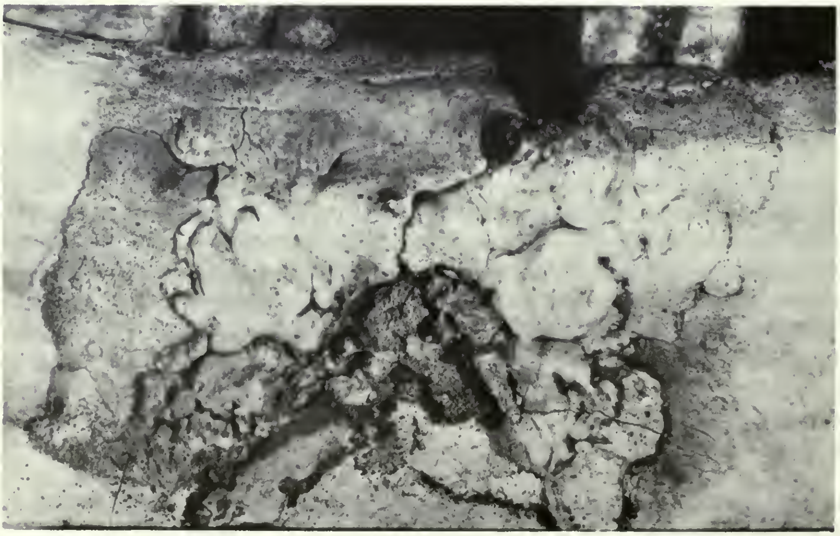

Fig. 3 Petrie horse. Detailed view of exostosis on ramus. (Photo: Royal Veterinary College.)

course of his excavations and of which he often wrote eloquently in his journals, the animal remains must have seemed commonplace and, though in many instances worthy of retention, unworthy of special note. Similarly, the important botanical materials that Petrie found, some of which are also in the collections of the British Museum (Natural History), appear to have received scant mention in his records. It is perhaps difficult to comprehend this today, with the present emphasis on reconstruction of the environment and economy of earlier human populations from exactly this kind of evidence rather than from the more material remains. Such a commentary takes no account of course of the scale of Petrie's work, its pioneer character, the huge and important collections that he made and distributed to museums in many parts of the world, and the immense volume of material that he published over a long life of ceaseless work. He was in fact one of the principal founders of modern archaeology. Fortunately he did record some of the skeletal material he found as exemplified by the following passage from *Gizeh and Rifeh* (Petrie, 1907):

> In the cemetery some tombs full of animals' skeletons were found. All the skulls in good state were preserved, and sent to the British Museum (Natural History). Mr. Oldfield Thomas has kindly given the following report upon them: "The skulls form a wonderfully fine set, which will no doubt prove of great value when some one arises with time and taste to work out such things in detail. I never saw so fine a series before. There are 192 cats' skulls, mostly *Felis ocreata*, but no doubt some are *F. chaus*. They are, however, a wonderfully varying lot, and would require much work for every one to be certainly and exactly determined. One might believe that the Ancient Egyptians had as many different kinds as we have now. Also 7 mongoose skulls (*Mungos ichneumon*), 3 wild-dog (*Canis lupaster*), and 1 fox (*Vulpes famelica*)."

The series of 192 cats' skulls was later described by Morrison-Scott (1952) but the rest of the collections presented by Petrie to the British Museum (Natural History) remain to be studied. Although much of this material lacks documentation we are optimistic that further information may yet come to light. We intend to subject more specimens to radiocarbon dating in the belief that this will yield interesting results and contribute to our knowledge of the history of domesticated animals in Egypt. Petrie died in 1942, a decade before the advent of radiocarbon dating but doubtless its application to material he collected would have greatly interested and gratified him. The continuing need to retain excavated skeletal material for possible future investigation cannot be overstressed. In the present instance, the precise dating of the horse skeleton has endowed it with a scientific value which Sir Flinders Petrie would have been the first to applaud.

Appendix

Pathological examination of the mandible of the Petrie horse

A region of prominent exostosis on the left mandibular ramus of the horse (Figs 2 and 3) was kindly examined for us by Dr E. C. Appleby of the Pathology Department, Royal Veterinary College, London, who reported as follows:

> Part of the mineralized material forming a plaque on the mandibular surface near the base of the cheek teeth was removed and decalcified for histological examination. This revealed a trabecular structure suggestive of new, superficial bone growth possibly overlying a lesion deeper in the bone. The exostosis appears to have been inflammatory in origin and may have been the result of an abscess at the base of a tooth or perhaps due to traumatic or other injury to the periosteum. Somewhat similar, but much smaller, deposits elsewhere on the mandible were not examined histologically. The condition had evidently been established for some weeks. Bone changes of this kind are not uncommon in horses although usually associated with chronic degenerative diseases of the joints rather than present in the facial region. Lesions on the mandible of horses can occur as part of a generalized skeletal change associated with space-occupying lesions in the chest (acropachia) but, as stated in the main text above, in this case all the other surviving bones of the horse were healthy in appearance.

Acknowledgements

We thank Mrs Barbara Adams and Dr D. M. Dixon of the Department of Egyptology, University College London, and Miss Mary Crawford of the Egypt Exploration Society for kindly allowing us to consult records in their care.

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Manuscript accepted for publication 7 September, 1977

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G. A. Boxshall

Zoology series Vol 35 No 3 26 April 1979

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ISSN 0007-1498

Zoology series
Vol 35 No 3 pp 201-264

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 26 April 1979

The planktonic copepods of the northeastern Atlantic Ocean: Harpacticoida, Siphonostomatoida and Mormonilloida

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Synopsis

Diagnoses of 17 species of planktonic harpacticoids are given, including two new mesopelagic genera, *Volkmannia* and *Neotisbella*, and 3 new species, *Volkmannia forficula*, *V. attenuata* and *Neotisbella gigas*, belonging to the family Tisbidae. The new genera are related to the genus *Bathyidia* Farran, and the male of the type species of this genus, *B. remota* Farran, is described for the first time. Ten species of planktonic siphonostomatoids are described, including 6 new bathypelagic species belonging to the genus *Hyalopontius* Sars (= *Megapontius* Hulsemann). The new species are *H. hulsemannae*, *H. alatus*, *H. spinatus*, *H. roei*, *H. cinctus* and *H. enormis*. The 2 species of *Mormonilla* Giesbrecht are described and the systematic position of this aberrant genus is considered. It is proposed to raise the family Mormonillidae to a new order, the Mormonilloida, derived from the podoplean line within the Copepoda.

Introduction

This revision of the minor planktonic copepod orders occurring in the northeastern Atlantic was prompted by the discovery of two new genera of planktonic harpacticoids and of six new

Bull. Br. Mus. nat. Hist. (Zool.) **35** (3) : 201–264 Issued 26 April 1979

species of free-living bathypelagic siphonostomatoids. Good descriptions of the representatives of the minor orders, Harpacticoida, Siphonostomatoida and Mormonilloida, are often not available or are not readily accessible to plankton workers who tend to concentrate on the more dominant groups. Consequently, these groups are comparatively poorly studied and published data on occurrence, depth distribution and other aspects of their biology are scarce.

Materials and methods

This study is based on a day and night series of hauls taken at 'Discovery' station 7089 in the region of the Cape Verde Islands (18° N 25° W) using the RMT 1+8 net system. The details of hauls and the fractions examined are given in Boxshall (1977). The *Hyalopontius* material was caught using the same net system in the northeastern Atlantic at a number of stations fished between 1974 and 1977. Dr Howard Roe (I.O.S.) isolated the *Hyalopontius* material from these latter samples and kindly allowed me to work them up. The type material of several of the species redescribed below and other specimens from important collections were also examined. All the specimens examined are stored in the British Museum (Natural History); a maximum of ten registration numbers is assigned to any one species-collection. Body lengths were measured from the tip of the rostrum to the distal end of the caudal rami excluding the caudal setae, except in *Aegisthus* Giesbrecht. In this genus body length was measured from the base of the rostrum to the proximal end of the very elongate caudal rami.

Key to planktonic species belonging to the Harpacticoida, Siphonostomatoida and Mormonilloida found in the northeastern Atlantic Ocean

1	Leg 5 present; second antenna exopod at most 4-segmented, sometimes absent	2
–	Leg 5 absent; second antenna exopod 8-segmented	**(*MORMONILLOIDA*)** 21
2	Mandible stylet-like, located within an oral cone, without palp; inner seta present on coxa of legs 1–4	**(*SIPHONOSTOMATOIDA*)** 18
–	Mandible not stylet-like, usually with palp; coxal seta absent	**(*HARPACTICOIDA*)** 3
3	First thoracic somite free (prosome 5-segmented)	4
–	First thoracic somite fused to cephalothorax (prosome 4-segmented)	5
4	Dorsal surface of prosome without chitinous markings; rostrum absent in ♂, long in ♀; first antenna 6-segmented in ♀	***Aegisthus mucronatus***
–	Dorsal surface of prosome without chitinous markings; rostrum short in ♀; first antenna 7-segmented in ♀	***Aegisthus spinulosus***
–	Dorsal surface of prosome with chitinous markings; rostrum short in both sexes; first antenna 7-segmented in both sexes	***Aegisthus aculeatus***
5	Body small, fusiform (Figs 2A, B), without marked boundary between prosome and urosome; caudal rami short; leg 1 with 3-segmented rami	6
–	These characters not combined	7
6	Body length 0·3–0·6 mm; inner caudal seta about 3 times longer than outer caudal seta and usually about as long as body	***Microsetella norvegica***
–	Body length 0·6–0·9 mm; inner caudal seta 7–10 times longer than outer seta and usually more than 1·5 times longer than body	***Microsetella rosea***
7	Both rami of leg 1 2-segmented	***Euterpina acutifrons***
–	At least one ramus 3-segmented	8
8	Leg 1 exopod 3-segmented; second antenna exopod 4-segmented; second maxilla reduced to basal segment with 1 seta and terminal claw (as Fig. 4F)	9
–	These characters not combined	12
9	Leg 1 endopod 2-segmented	***Neotisbella gigas*** sp. nov.
–	Leg 1 endopod 3-segmented	10
10	Third endopod segment of leg 1 comprising about 14% of length of ramus; mandible endopod with 2 proximal and 5 apical setae	***Bathyidia remota***
–	Third endopod segment of leg 1 comprising about 3–5% of length of ramus; mandible endopod with 3 proximal and 6 apical setae	11
11	Endopod of leg 1 about 34% longer than exopod	***Volkmannia forficula*** sp. nov.
–	Endopod of leg 1 about 70% longer than exopod	***Volkmannia attenuata*** sp. nov.

12	Maxilliped very squat and robust; leg 1 rami 3-segmented	*Parathalestris croni*
–	Maxilliped slender; one ramus of leg 1 with less than 3 segments	13
13	Leg 1 with 3-segmented endopod and 1-segmented exopod	14
–	Leg 1 with 2-segmented endopod and 3-segmented exopod	15
14	First antenna 8-segmented; leg 1 exopod with 4 setae	*Clytemnestra scutellata*
–	First antenna 7-segmented; leg 1 exopod with 3 setae	*Clytemnestra rostrata*
15	Cephalosome with a pair of large cuticular lenses	16
–	Cephalosome without cuticular lenses	*Macrosetella gracilis*
16	Exopod of second antenna 1-segmented with 2 distal setae	17
–	Exopod of second antenna absent	*Oculosetella gracilis*
17	Baseoendopod of leg 5 with 5 setae in ♂, 3 in ♂	*Miracia efferata*
–	Baseoendopod of leg 5 with 4 setae in ♀, 2 in ♂	*Miracia minor*
18	First antenna 11-segmented in both sexes	*Hyalopontius* (see p. 244)
–	First antenna 5- to 9-segmented	19
19	Second antenna exopod absent; leg 5 with free segment	20
–	Second antenna exopod 1-segmented; leg 5 without free segment	*Pontoeciella abyssicola*
20	First antenna 5-segmented in ♀, 7-segmented in ♂	*Ratania flava*
–	First antenna 7-segmented in ♀, 9-segmented in ♂	*Ratania atlantica*
21	First antenna 3-segmented; lateral seta of caudal ramus located about 33% of distance along ramus	*Mormonilla phasma*
–	First antenna 4-segmented; lateral seta of caudal ramus located about 16% of distance along ramus	*Mormonilla minor*

Description of species

HARPACTICOIDA

A total of 17 species belonging to 7 families are regarded here as being true planktonic forms. Many other harpacticoids have been recorded from the plankton, but they have usually been found in the neritic zone and can be regarded as temporarily displaced littoral forms (Wells, 1970). Occasionally littoral species are carried into oceanic waters by clinging to algae drifting in ocean currents (Yeatman, 1962), these can also be regarded as expatriated specimens as they are not permanent members of the plankton.

Family **AEGISTHIDAE**

Genus ***AEGISTHUS*** Giesbrecht, 1891

Diagnosis. Prosome 5-segmented with first thoracic somite free and about equal in size to the following somite. Genital complex (♀) with dorsal and lateral transverse suture line. Caudal rami at least twice as long as whole body. Rostrum present or absent. First antenna (♀) 6- or 7-segmented, (♂) 7- or 8-segmented, weakly or not geniculate. Second antenna slender with 1-segmented exopod bearing 1 or 2 setae. Mandible (♀) with or without rudimentary palp; apparently absent in ♂. First maxilla (♀) well developed, (♂) bilobed, rudimentary. Second maxilla (♀) well developed, (♂) with well-developed basipod but rudimentary rami. Maxilliped 3-segmented; (♀) well developed, (♂) poorly developed. Legs 1–4 with 3-segmented rami, armature formula as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1–I	0–1; 0–1; 1, 2, 2	I–1; I–1; I, 2, 2
Leg 2	0–0	1–0	0–1; 0–2; 1, 2, 2	I–1; I–1; III, 2, 2
Leg 3	0–0	1–0	0–1; 0–2; 1, 2, 3	I–1; I–1; III, 2, 2
Leg 4	0–0	1–0	0–1; 0–1; 1, 2, 2	I–1; I–1; III, 2, 3

Leg 5 elongate, bearing a short naked seta and 5 serrate setae (♀) and with 5 serrate setae and 2 additional plumose setae in ♂. Leg 6 with 1 or 2 small setae.

TYPE-SPECIES. *Aegisthus mucronatus* Giesbrecht, 1891.

REMARKS. Some differences of opinion exist over the homology of the caudal rami in this well-defined genus. Giesbrecht (1892), Scott (1894), Farran (1905), Rose (1933) and Wells (1970) have erroneously interpreted the structures on the anal somite as comprising very short caudal rami fused to the anal somite and each bearing an extremely long seta which is itself setate (see Scott, 1894; pl. 11, figs 31 & 44). In fact the caudal rami are extremely long (often as much as five times longer than the body), closely pressed together and armed with a lateral seta in the middle third of each ramus and at least 2 apical setae, one of which is plumose (Sars, 1916; Lang, 1948).

Aegisthus mucronatus Giesbrecht, 1891

Aegisthus mucronatus Giesbrecht, 1891 : 476.
A. longirostris Scott, 1894 : 104, pl. XI, figs 31–44.
A. dubius Sars, 1916 : 8, 14, pl. VIII.

DIAGNOSIS. *Female.* Prosome without reticulate chitinous markings on dorsal surface; maximum body width at level of second free thoracic somite (Fig. 1A). Genital complex with dorsal and lateral transverse suture line, armed with spinules. Rostrum very long and anteriorly directed. First antenna 6-segmented with large hook-like process medially on proximal segment. Second antenna with 2 unequal distal setae on exopod. Maxilliped (Fig. 1B) 3-segmented with 3 enlarged spines and 1 seta on middle segment and 3 setae on distal segment. Leg 1 with 3-segmented rami, but suture lines between segments 2 and 3 sometimes indistinct; exopod segments 2 and 3 with short spines on outer margins. Leg 5 (Fig. 1C) free segment with 3 serrate setae on lateral margin, 1 serrate seta and a naked seta distally and 1 serrate seta subapically. Leg 6 (Fig. 1D) an elongate free segment with a short subapical and a long apical seta.

Body length of female from 1·90 to 2·55 mm.

Male. As ♀ except: cephalothorax (Fig. 1E) relatively narrow. Rostrum absent. First antenna 8-segmented. Second antenna (Fig. 1F) with 1 seta distally on exopod. First maxilla bilobed, rudimentary. Second maxilla with large claw-like process on basipod, rami rudimentary with 5 short setae. Maxilliped 3-segmented; weakly developed, carrying 2 short setae on apex of distal segment. Leg 5 (Fig. 1G) 2-segmented; first segment with small proximal seta and distal serrate seta on outer margin; second segment with 2 serrate seta on outer margin, 2 on distal margin (the inner just longer than the outer) and 2 plumose setae on inner margin.

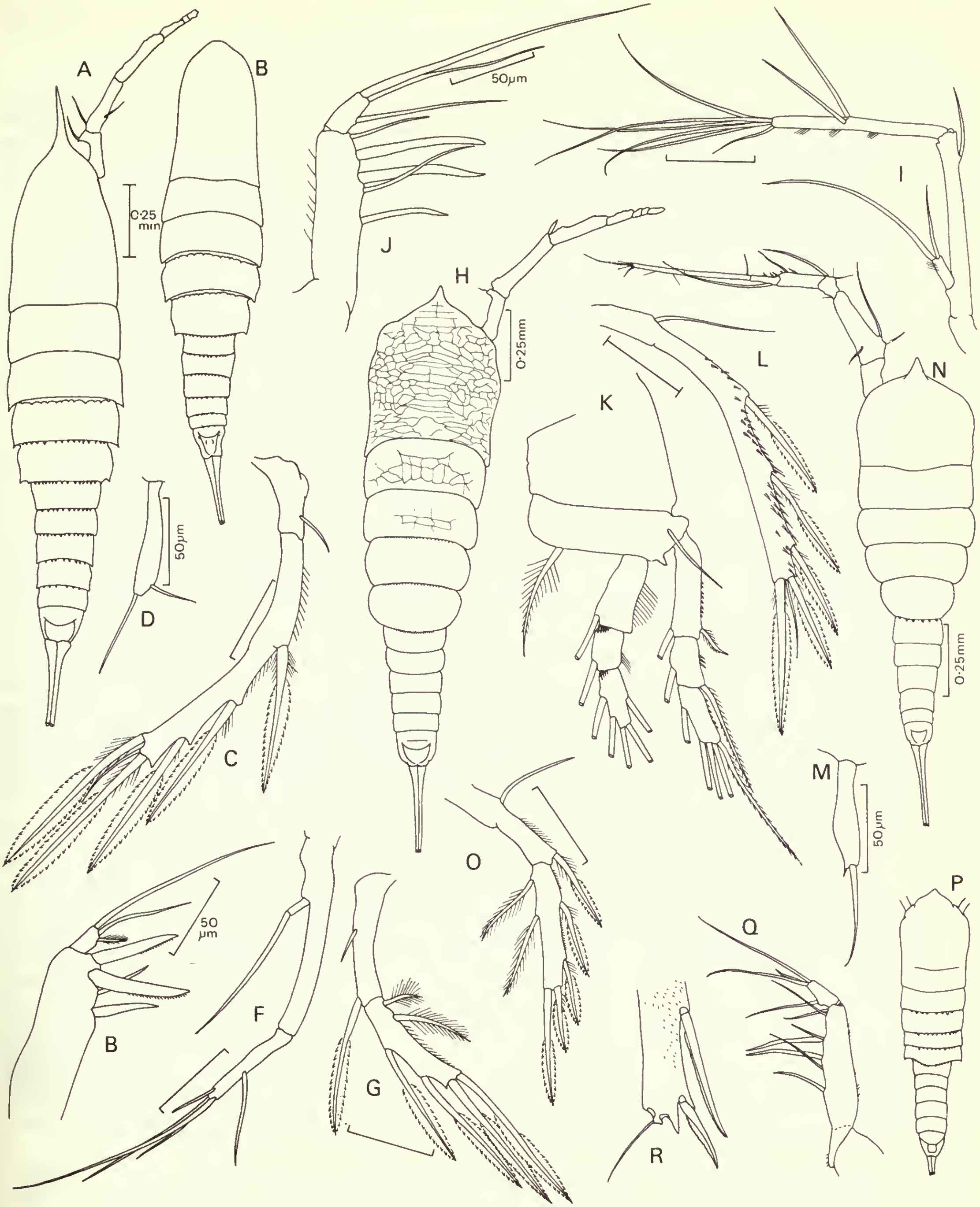
Body length of male from 1·10 to 1·70 mm.

MATERIAL EXAMINED. 352 ♀♀, 48 ♂♂: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.155–164 (♀) and 1977.165–174 (♂). 3 ♀♀, 1 ♂ syntypes of *A. longirostris*: Gulf of Guinea, 1° 55′ N 5° 55′ E (Scott, 1894). BM(NH) registration numbers 1893.4.22.588–589.

REMARKS. Sars (1916) described *A. dubius* from male specimens and mentioned the similarities between it and female *A. mucronatus*. He regarded it as a separate species because of the absence of a rostrum, the structure of the first antenna and the marked reduction of the mouthparts. Farran (1926) suspected that *A. dubius* was the male of *A. mucronatus*, as *A. mucronatus* females were found in every haul from which *A. dubius* was recorded but he did not synonymize the two species because Scott (1894) had described both sexes of a new species, *A. longirostris*, the females of which had since been recognized as being synonymous with *A. mucronatus*. The syntype series of *A. longirostris* contains only 1 male specimen. This specimen lacks a rostrum and its appendages are as described by Sars (1916) for *A. dubius*. The arostrate males (*A. dubius* Sars, 1916) have been correctly regarded as the males of *A. mucronatus* by most authors since Lang (1948).

Aegisthus aculeatus Giesbrecht, 1891

DIAGNOSIS. *Female.* Cephalothorax and free thoracic somites with conspicuous reticulate markings (Fig. 1H); maximum width of body near mid-point of cephalothorax. Genital complex subdivided


A
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0·25mm
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P
Q
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F
G
R

Fig. 1 *Aegisthus mucronatus*: A, female; B, maxilliped; C, fifth leg; D, sixth leg; E, male; F, second antenna; G, fifth leg. *A. aculeatus*: H, female; I, second antenna; J, maxilliped; K, first leg; L, fifth leg; M, sixth leg; N, male; O, fifth leg. *A. spinulosus*: P, female; Q, maxilliped; R, tip of fifth leg. (P–R redrawn from Farran, 1905.) Scales 0·1 mm unless otherwise indicated.

dorsally and laterally by suture line. First antenna 7-segmented with small prominence medially on proximal segment. Second antenna (Fig. 1I) with 2 distal setae on exopod. Maxilliped (Fig. 1J) 3-segmented, bearing 3 enlarged spines and 2 slender setae on middle segment and 3 setae on distal segment. Leg 1 (Fig. 1K) with 3-segmented rami, exopod segments 2 and 3 with long spines on outer margin. Leg 5 (Fig. 1L) free segment with 3 serrate setae on outer margin and a short naked seta and 2 serrate setae on the distal margin; distal serrate seta on lateral margin 83% as long as middle serrate seta on lateral margin; inner apical seta 35–40% longer than outer. Leg 6 (Fig. 1M) an elongate free segment with a single long seta and a minute spinule apically.

Body length of female from 1·64 to 1·85 mm.

Male. As for ♀ except: prosome more squat in appearance (Fig. 1N); second free thoracic somite as wide as cephalothorax. First antenna 7-segmented. First maxilla bilobed, rudimentary. Second maxilla with well-developed basipod, claw-like process on basipod less curved than in ♂ *A. mucronatus*, rami rudimentary bearing 1 small and 5 long setae. Maxilliped 3-segmented, slender, with 2 setules on middle segment and 3 setae on distal segment. Leg 5 (Fig. 10) with armature elements as in ♂ *A. mucronatus* but inner distal margin seta about 35–40% longer than outer. Leg 6 with 2 long setae.

Body length of male from 1·28 to 1·35 mm.

MATERIAL EXAMINED. 154 ♀♀, 7 ♂♂: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.175–184 (♀) and 1977.185–191 (♂).

REMARKS. The male of *A. aculeatus* has only recently been discovered and partially described (Owre and Foyo, 1967). The mouthparts in male *Aegisthus* are reduced and are often difficult to observe. No structure was found in either *A. aculeatus* or *A. mucronatus* which could be positively identified as representing the mandible. The first maxilla was represented by a bilobed structure in males of both species; the larger lobe bearing 5 or 6 setae and the smaller 1 or 2. The second maxilla has a well-developed basipod and distal claw but the rami are reduced. The maxilliped is 3-segmented in both species. In *A. aculeatus* males the middle segment bears 2 setules and the distal segment 2 naked medial setae and a plumose apical seta. Reduction of this appendage has proceeded further in male *A. mucronatus* with the armature comprising only 2 small setae on the distal segment. The second maxillae and maxillipeds are better developed and closer to the female condition in *A. aculeatus* males than in *A. mucronatus* males.

Aegisthus spinulosus Farran, 1905

DIAGNOSIS. *Female*. Cephalothorax and free thoracic somites without chitinous reticulations (Fig. 1P); maximum width of body anterior to mid-point of cephalothorax. Rostrum short. Genital complex completely subdivided by suture line. First antenna 7-segmented. Second antenna and both maxillae as in *A. aculeatus*. Maxilliped (Fig. 1Q) 3-segmented, armed with 3 enlarged spines and 4 setae on middle segment and 4 setae on distal segment. Leg 1 with 3-segmented rami; exopod segments 2 and 3 with long spines on outer margins. Leg 5 (Fig. 1R) as in *A. aculeatus* except distal serrate seta on lateral margin only 57% as long as middle serrate seta on lateral margin. Leg 6 with 2 equal terminal setae.

Body length of holotype ♀ 1·74 mm.

MATERIAL EXAMINED. None.

REMARKS. In the original description of *A. spinulosus* Farran (1905) commented on its close affinity to *A. aculeatus*, but listed certain important characters which serve to distinguish between them. The significant differences are the absence of chitinous reticulations from the cephalothorax, the complete subdivision of the genital complex, the armature of the maxilliped (called the first maxillipede by Farran) and the sixth leg. If Farran's (1905) description is accurate *A. spinulosus* should be regarded as a valid species and not, as suggested by Lang (1948), as a possible last copepodid stage of *A. aculeatus*.

Family ECTINOSOMATIDAE

Genus *MICROSETELLA* Brady and Robertson, 1873

DIAGNOSIS. Body fusiform, without marked boundary between prosome and urosome; prosome 4-segmented with first thoracic somite fused to head, urosome 5-segmented. Rostrum very short, ventrally directed. Caudal rami short, each with a long apical seta. First antenna 6-segmented (Fig. 2C), with an aesthete on segment 3 or 4 and one on segment 6. Second antenna (Fig. 2D) with unarmed basis; exopod 3-segmented with single short seta on segment 1 and 2 long terminal setae. Mandible (Fig. 2E) blade with few weak teeth; palp well developed, exopod small with few setae, endopod large bearing several setae and a large unilaterally pinnate process (seta ?) with an apical seta. First and second maxillae (Figs 2F, G) small. Maxilliped (Fig. 2H) 3-segmented, robust. Legs 1–4 with 3-segmented rami, armature formula:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1–0	0–1; 0–1; I, 2, 2	I–0; I–1; II, 2, 1
Leg 2	0–0	1–0	0–1; 0–1; I, 2, 2	I–1; I–1; II, 2, 2
Leg 3	0–0	1–0	0–1; 0–1; I, 2, 2	I–1; I–1; II, 2, 3
Leg 4	0–0	1–0	0–1; 0–1; I, 2, 2	I–1; I–1; II, 2, 3

Leg 5 with baseoendopod and 1-segmented exopod; exopod bearing 1 ventral surface seta and either 3 (♀) or 2 (♂) marginal setae.

TYPE SPECIES. *Microsetella norvegica* (Boeck, 1864) (as *M. atlantica* Brady and Robertson, 1873).

Microsetella norvegica (Boeck, 1864)

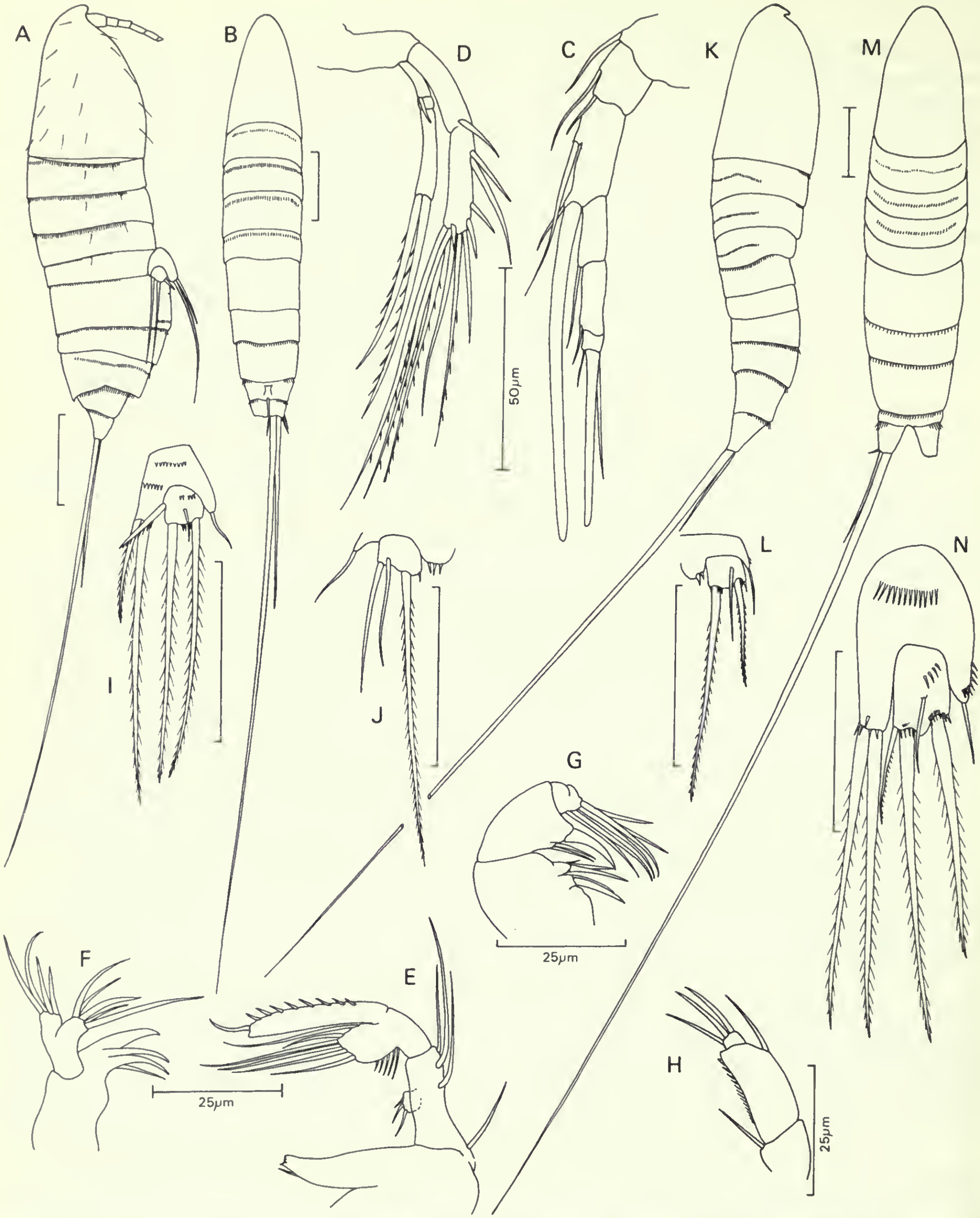
Setella norvegica Boeck, 1864 : 281.
Microsetella atlantica Brady and Robertson, 1873 : 130, pl. IX, figs 11–16.
Ectinosoma atlanticum Brady, 1880: 13, pl. 38, figs 11–19.

DIAGNOSIS. Longest seta (inner seta on distal margin) of caudal ramus usually about as long as body, sometimes up to 1·5 times longer than body (Figs 2A, B); the second longest seta (outer seta on distal margin) about 33% as long as the longest caudal seta and between 0·3 and 0·5 times as long as body. Inner seta on baseoendopod of leg 5 (♀) less than half as long as outer seta (Fig. 2I). Lateral seta on distal margin of leg 5 exopod (♂) apparently naked (Fig. 2J).

Body length of female 0·35–0·57 mm; body length of male 0·33–0·42 mm.

MATERIAL EXAMINED. 2 ♀♀: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.192–193. 1 ♀: as *Ectinosoma atlanticum*, Faroe Channel. BM(NH) registration numbers 1901.9.27.101–2. 1 ♀, 1 ♂: Suez Canal Expedition (Gurney, 1927). BM(NH) registration number 1928.4.2.137. 5 ♀♀: as *E. atlanticum*, Loch Fyne. BM(NH) registration numbers 1956.9.25.45. 12 ♀♀: North Sea off Whitby. BM(NH) registration numbers 1976.653–662.

REMARKS. This small species is usually distinguished from the only other species of the genus, *M. rosea* (Dana, 1848), by the relative length of the body and the longest seta on the caudal ramus. This seta is often shorter than or about as long as the whole body (Lang, 1948; Owre & Foyo, 1967; Wells, 1970). However, in the material examined during the present study the length of the longest caudal seta was found to vary from 20% less than body length to 44% more than body length (Table 1). More reliable characters which could be used to separate the species are body size, the armature of the baseoendopod in the female leg 5 and the relative length of the second longest (outer seta on distal margin) caudal seta. This outer caudal seta is about one third (33%) as long as the inner caudal seta in *M. norvegica*.


A
B
D
C
K
M
50μm
I
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L
N
G
25μm
F
E
25μm
H
25μm

Fig. 2 *Microsetella norvegica*: A, female, lateral; B, female, dorsal; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped; I, fifth leg; J, male fifth leg. *M. rosea*: K, male; L, fifth leg; M, female; N, fifth leg. Scales 0·1 mm unless otherwise indicated.

Table 1 Body and caudal seta lengths of examined specimens of *Microsetella*

Locality	Number examined	(A) Body length in mm	(B) Caudal seta length in mm	Ratio A : B
Microsetella norvegica				
'Discovery' Stn 7089	1 ♀	0·57	0·82	1 : 1·44
Faroe channel	1 ♀	0·57	0·59	1 : 1·04
Suez canal	1 ♂	0·33	0·28	1 : 0·85
Loch Fyne	5 ♀	0·52	0·43	1 : 0·83
		0·50	0·43	1 : 0·86
		0·50	0·43	1 : 0·86
		0·41	0·33	1 : 0·80
		0·50	0·44	1 : 0·88
Off Whitby	12 ♀	0·44	0·43	1 : 0·98
		0·43	0·41	1 : 0·95
		0·44	0·44	1 : 1
		0·41	0·39	1 : 0·95
		0·46	0·39	1 : 0·85
		0·43	0·43	1 : 1
		0·43	0·41	1 : 0·95
		0·46	0·44	1 : 0·96
		0·43	0·46	1 : 1·07
		0·43	0·41	1 : 0·95
		0·41	0·43	1 : 1·05
		0·41	0·41	1 : 1
Microsetella rosea				
Gulf of Guinea	2 ♀	0·67	1·17	1 : 1·75
		0·69	1·26	1 : 1·83
Hyeres	1 ♀	0·65	1·22	1 : 1·88
Off Co. Mayo	1 ♂	0·63	0·96	1 : 1·52

Microsetella rosea (Dana, 1848)

Harpacticus rosea Dana, 1848: 153.
Microsetella rosea Giesbrecht, 1891 : 476.

Diagnosis. Longest seta (inner seta on distal margin) of caudal ramus from 1·5 to 2 times as long as body (Figs 2K, M); second longest seta (outer seta on distal margin) about 10–15% as long as longest caudal seta and between 0·20 and 0·25 times as long as the body. Inner seta on baseoendopod of leg 5 (♀) about the same length as outer seta (Fig. 2N). Lateral seta on distal margin of leg 5 exopod (♂) bilaterally spinulate (Fig. 2L). Body length of female 0·64–0·85 mm; body length of male 0·6–0·7 mm.

Material examined. 2 ♀♀: as *M. atlanticum*. Gulf of Guinea (Scott, 1894). BM(NH) registration numbers 1893.4.22.219–223. 1 ♀: as *M. atlanticum*. Hyeres. BM(NH) registration number 1951.11.24.35. 1 ♂: off Co. Mayo (Farran, 1908). BM(NH) registration number 1911.11.8.42881.

Remarks. Both sexes of *M. rosea* are much larger than in *M. norvegica*. Other characters which can be used to separate the species are the relative lengths of the two main caudal setae, the ratio of caudal seta length to body length (see Table 1) and the armature of the baseoendopod of the (♀) leg 5.

Family TISBIDAE

Genus *BATHYIDIA* Farran, 1926

Diagnosis. Body not laterally compressed (Fig. 4A). Prosome 4-segmented, urosome 5-segmented in ♀, 6-segmented in ♂. Dorsal surface of prosome and whole surface of urosome more or less

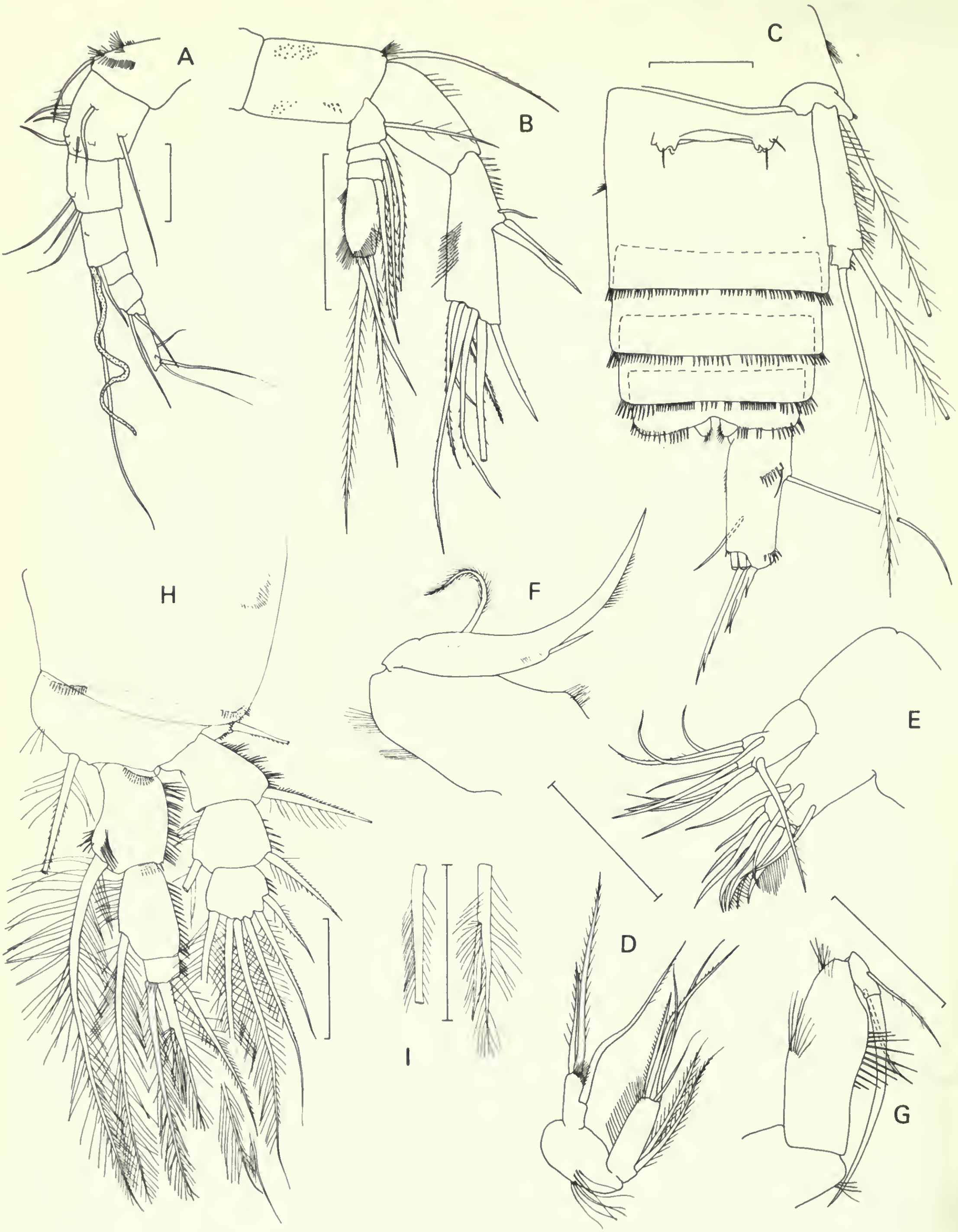

Fig. 3 *Bathyidia remota*, holotype female: A, first antenna; B, second antenna; C, urosome; D, mandible 'palp'; E, first maxilla; F, second maxilla; G, maxilliped; H, first leg; I, middle setae of third endopod segments from both first legs. Scales 0·1 mm.

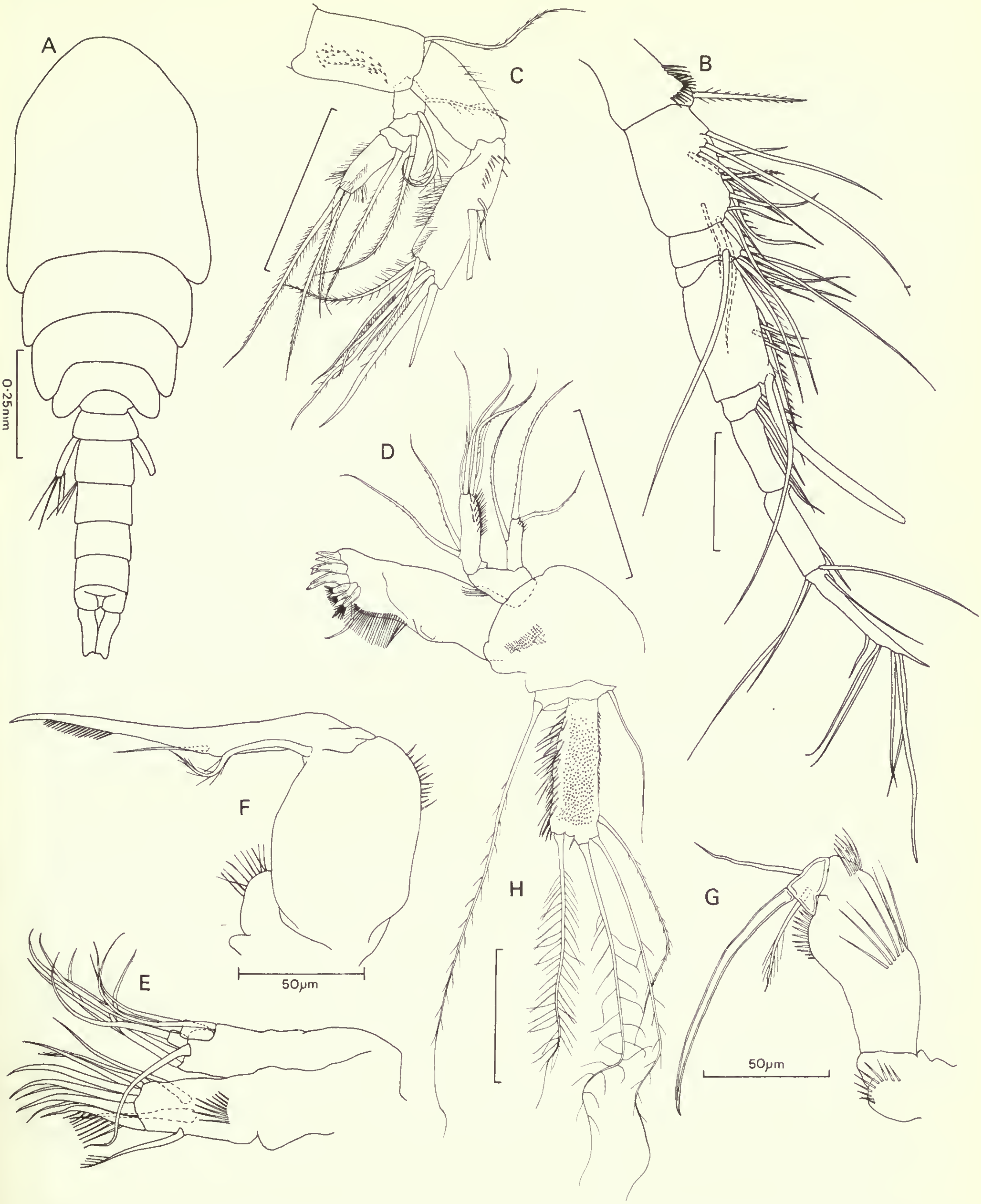
A
B
C
D
E
F
G
H
0·25mm
50μm
50μm

Fig. 4 *Bathyidia remota* male: A, dorsal; B, first antenna; C, second antenna; D, mandible; E, first maxilla; F, second maxilla; G, maxilliped; H, fifth leg. Scales 0·1 mm unless otherwise indicated.

covered with minute denticles. Genital complex (♀) subdivided by a dorsal and dorso-lateral suture line. Genital area probably with 3 short setae either side of oviduct openings (only 2 setae remaining in holotype ♀). Caudal rami more than twice as long as wide; with 2 lateral, 1 dorsal and 4 distal setae plus 2 additional elements on the distal margin.

First antenna 8-segmented (♀) with aesthete on segment 4; 9-segmented (♂) with aesthete on segment 5, geniculate between segments 7 and 8. Second antenna (Figs 3B, 4C) with 1 seta on basis; 2-segmented endopod, distal segment with 3 lateral and 7 terminal elements; 4-segmented exopod with segment 1 bearing 2 setae, segments 2 and 3 bearing 1 seta each and the distal segment with 3 setae. Mandible (Figs 3D, 4D) with unarmed basis and 1-segmented rami; endopod with 2 proximal setae on medial margin and 5 apical setae; exopod with 1 medial and 2 apical setae. First maxilla (Figs 3E, 4E) inner lobe (arthrite) armed with 11 elements, outer lobe including rudimentary rami bearing 10 elements. Second maxilla (Figs 3F, 4F) with 1 seta on basal segment, claw elongate bearing a spiniform seta and a distal row of pinnules. Maxilliped (Figs 3G, 4G) comprising 3-segments and a terminal claw; middle segment with 3 rows of setules, distal segment with 2 setae; displaying dimorphism with the distal segment bearing a strong chitinous process in ♂.

Legs 1–4 with 3-segmented rami; armature formula as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1–I	0–1; 0–1; 3	1–0; 1–1; 6
Leg 2	0–0	1–0	0–1; 0–2; I, 2, 2	I–1; I–1; III, I, 3
Leg 3	0–0	1–0	0–1; 0–2; I, 2, 3	I–1; I–1; III, I, 4
Leg 4	0–0	1–0	0–1; 0–2; I, 2, 2	I–1; I–1; III, I, 4

Leg 1 endopod 20–25% longer than exopod; basis with spinulate lobe between bases of rami; inner spine on basis setiform; spines on outer margins of exopod segments 1 and 2 also setiform. Leg 2 displaying sexual dimorphism in structure of inner seta on (♂) endopod segment 1. Legs 1–4 with minute denticles on surface, especially on lateral surface of coxa and on both anterior and posterior surfaces of rami; also spinule rows present on posterior surfaces of endopod segments 2 and 3.

Leg 5 with small baseoendopod and elongate free segment; baseoendopod with outer plumose seta and single inner seta; armature of free segment consisting of 1 distal seta on inner and outer margins and 2 setae and a tiny setule around apex.

Leg 6 represented by 3 naked setae in ♂.

Type-species. *Bathyidia remota* Farran, 1926.

Remarks. The genus *Bathyidia* was established by Farran (1926) to include a new bathypelagic species from the Bay of Biscay, *B. remota*. Farran's (1926) description of *B. remota* was incomplete. The generic diagnosis given here is based on re-examination of the holotype of *B. remota* and on the examination of two male specimens. *Bathyidia* is related to both *Tisbe* Lilljeborg, 1853 and *Paraidya* Sewell, 1940, as well as to the two new genera described below *Neotisbella* gen. nov. and *Volkmannia* gen. nov. The principal distinguishing characters of these five genera and the genera *Tisbella* Gurney 1927 and *Tisbintra* Sewell, 1940 are presented in Table 2. *Bathyidia* can readily be distinguished from *Paraidya* by the segmentation of the first antenna, and from *Neotisbella* and *Tisbella* by the segmentation of the endopod of leg 1. The differences between *Bathyidia*, *Tisbe* and *Volkmannia* are the armature of the mandibular palp, the relative size of the endopod segments of leg 1, the armature elements of both rami of leg 1, plus the structure and armature of the caudal rami.

Bathyidia remota Farran, 1926

Bathyidia remota Farran, 1926: 299–300, pl. 10, figs 13–17.
Tisbe remota Lang, 1948 : 383, pl. 168, fig. 6.

Diagnosis. Prosome of ♀ incompletely known, ♂ cephalothorax slightly indented laterally (Fig. 4A). Genital complex (♀) and urosome somites 3, 4, 5 and 6 (in ♂) provided with ventral and ventrolateral rows of spinules along posterior borders (Figs 3C and 5G). Genital area (♀) (Fig. 3C) with 2 short naked setae either side of oviduct openings, a third seta was probably present but is missing from the holotype ♀. Caudal ramus (Figs 3C and 5G) 2·2–2·6 times longer than greatest width; armed with 2 lateral setae in proximal half of ramus (the lateral being 6·6–6·9 times longer than the ventro-lateral one), an oblique spinule row on the ventral surface extending distally from bases of the lateral setae, another spinule row proximal to the outer distal angle, a naked seta on the dorsal surface, a seta at the outer distal angle and one at the inner distal angle, 2 long setae on the inner portion of the distal margin and 2 elements towards the outer end of the distal margin. The latter 2 elements are flaccid and subdivided giving a forked appearance.

Relative lengths of ♀ first antenna (Fig. 3A) segments 15 : 19 : 15 : 14 : 7 : 9 : 5 : 16. Armature elements incomplete, first segment with 2 spinule rows. First antenna of ♂ (Fig. 4B) with segmental armature elements as follows: I–1, II–14, III–7, IV–2, V–6+1 aesthete, VI–3, VII–2, VIII–2, IX–9. First segment also bearing spinule row. Other cephalic appendages as in generic diagnosis.

Inner spine on basis of leg 1 (Figs 3H, 5A) with small distal pinnules and a few larger ones proximally; exopod segment 3 bearing 6 setiform elements, those on outer margin armed with shorter pinnules than those on distal margin; relative lengths of endopod segments about 46 : 40 : 14; outer element on endopod segment 3 setiform but armed with short pinnules, middle element a simple long plumose seta (holotype ♀ exhibits aberrant bifurcated condition on only one member of leg 1 pair (Figs 3H, I)), inner element a plumose seta similar in length to middle element.

Legs 2–4 (Figs 5B–F); exopod segment 3 with central patch of larger denticles on posterior surface (Fig. 5E); endopod segments 2 and 3 with some denticles and about 5 and 16 spinules respectively on their posterior surfaces (Fig. 5F). Leg 2 displaying sexual dimorphism with inner seta on endopod segment 1 armed with distal row of spinules (Fig. 5B).

Leg 5 of ♀ (Fig. 3C) with incomplete armature in holotype but traces of absent setae indicate armature similar to ♂. Leg 5 of ♂ (Fig. 4H) with single inner seta on baseoendopod about as long as free segment: free segment about 2·9 times longer than wide, its ventral surface covered with minute denticles and lateral surface with long spinules; bearing a plumose seta at distal end of expanded lateral margin; projecting distal margin with a tiny setule laterally and 2 long sparsely plumose setae apically; inner margin with single pinnate seta distally.

Leg 6 of ♂ (Fig. 5G) comprising 3 long naked setae situated laterally on genital lobes of urosome somite 2.

Body length of holotype ♀ 1·48 mm and ♂ 1·41 mm.

Material examined. Holotype ♀: Bay of Biscay (Farran, 1926). BM(NH) registration number 1926.12.6.41. 1 ♂: Sargasso Sea, Stn S (Deevey and Brooks, 1977). Florida State Museum collections. 1 ♂: N.E. Atlantic Ocean 18° N 25° W 'Discovery' Stn 7089. BM(NH) registration number 1977.225.

Remarks. The males here assigned to *B. remota* agree closely with the holotype ♀ in the characteristic structure and armature of the leg 1. The bifurcate nature of the middle seta on endopod segment 3 in the holotype is regarded as aberrant because the middle seta on the other member of the leg 1 pair, although broken, displays no trace of a bifurcation at the same position on the seta (see Fig. 3I). The mouthparts are generally very similar in the males and the female. The male maxilliped differs from the female in the structure of the third segment, but the male maxillipeds of *Neotisbella gigas* gen. et sp. nov. and *Volkmannia forficula* gen. et sp. nov. also exhibit this character whereas their respective females do not.

The 2 male specimens are almost identical to the female in the detailed armature of their caudal rami; in the position of the spinule rows and especially in the relative lengths of the two lateral setae. These and other similarities strongly suggest that the two males are conspecific with the holotype ♀ of *B. remota*.

Genus ***VOLKMANNIA*** gen. nov.

Diagnosis. Prosome 4-segmented, urosome 5-segmented in ♀ and 6-segmented in ♂. Dorsal

Table 2 A comparison between the seven genera of the *Tisbe* group

Character	*Paraidya*	*Tisbella**	*Tisbintra*†
General facies	Laterally compressed, elongate	As for *Tisbe*	As for *Tisbe*
First antenna ♀ : ♂	7 : 8	7/8 : 8	8 : 9
Second antenna	1 seta on basis; Exp 3- or 4-segmented, with 1, 0, 3 or 1, 1, 2, 3 elements	1 seta on basis; Exp 4-segmented with 1, 1, 1, 3 elements; segs 2 & 3 fused to seg. 4 in *T. pulchella*	1 seta on basis; Exp 2-segmented (segs 2, 3 & 4 fused) with 1, 2 proximal & 3 distal elements
Mandible	Basis unarmed, Enp with 3 medial & 6 distal setae, Exp with 2 setae	Basis unarmed, Enp with 3 medial & 7 distal setae, Exp with 2 setae	Basis with 1 small seta, Enp with 3 disto-medial & 5 or 6 distal setae, Exp with 2 setae
Maxilliped	Not exhibiting marked sexual dimorphism	Not exhibiting marked sexual dimorphism	Not exhibiting marked sexual dimorphism
Leg 1	3-segmented Enp less than 10% longer than Exp; Enp seg. 3 with 1 outer spine & 2 inner setae. Exp elements without combs of setules	2-segmented Enp; Enp seg. 2 with 1 outer spine, 2 distal setae & 1 inner seta. Exp elements without combs of setules	2-segmented Enp, about 60% longer than Exp; Enp seg. 2 with 1 inner seta & 1 or 2 distal elements. Exp elements without combs of setules
Leg 5	Free segment with 3 or 4 setae	Free segment with 5 plumose setae	Free segment with 4 or 5 setae
Caudal ramus	Less than 2·5 times longer than wide; with 6 elements including 1 lateral seta in distal half of ramus	As wide as long or just longer than wide; with 7 elements including 1 lateral seta in distal half of ramus	Shorter than wide; with 6 elements including 1 lateral seta in distal half of ramus

* Data from Yeatman (1963) and from re-examination of holotype ♀ of *Tisbella timsae* Gurney, 1927 from Imasili
Suez canal: BM(NH) registration number 1928.4.2.51.

† Data from Sewell (1940) and from examination of 2 ♀♀ & 2 ♂♂ specimens of *Tisbintra jonesi* Ummerkutty, 196
from Kuwait: BM(NH) registration numbers 1975.1201–1210.

surface of prosome and whole surface of urosome more or less covered with minute denticles. Rostrum small. Genital complex (♀) markedly subdivided by dorsal and dorso-lateral suture line, suture line absent ventrally; genital area with 1 short outer seta and 2 long naked setae either side of oviduct openings. Caudal rami about twice as long as wide, with 2 lateral, 1 dorsal and 4 distal setae plus 2 additional elements on the distal margin.

First antenna 8-segmented (♀) with aesthete on segment 4; 9-segmented (♂) with aesthete on segment 5, geniculate between segments 7 and 8. Second antenna with 1 seta on basis; 2-seg-

Tisbe	*Volkmannia*	*Neotisbella*	*Bathyidia*
Not usually elongate, dorso-ventrally flattened	As for *Tisbe*	Prosome vaulted	As for *Tisbe*
8:9	8:9	8:9	8:9
1 seta on basis; Exp 4-segmented with 1 or 2, 1, 1, 3 elements respectively	1 seta on basis, Exp 4-segmented with 2, 1, 1, 3 elements	Basis unarmed; Exp 4-segmented with 1, 0, 1, 3 elements	1 seta on basis; Exp 4-segmented with 2, 1, 1, 3 elements
Basis with 1 or more setae; Enp with 3 medial & 5 or 6 distal setae, Exp with 3 setae	Basis unarmed; Enp with 3 medial & 6 distal setae, Exp with 3 setae	Basis unarmed; Enp with 1 medial & 4 distal setae, Exp with 3 setae	Basis unarmed; Enp with 2 medial & 5 distal setae, Exp with 3 setae
Not usually exhibiting marked sexual dimorphism	Marked sexual dimorphism in segment 3	Marked sexual dimorphism in segment 3	Marked sexual dimorphism in segment 3
3-segmented Enp, usually distinctly longer than Exp; Enp seg. 3 with 2 or 3 elements 1 of which armed with comb of setules; similar combs on outer elements of Exp segs 2 & 3	3-segmented Enp 25–30% longer than Exp; Enp seg. 3 with 1 outer spine & 2 inner setae; Exp elements without combs of setules	2-segmented Enp about 10% longer than Exp; Enp seg. 2 with 1 outer spine, 2 distal setae & 1 inner seta; Exp elements without combs of setules	3-segmented Enp 20–25% longer than Exp; Enp seg. 3 with 2 setiform elements; Exp elements without combs of setules
Free segment with 4 or 5 setae	Free segment with 4 plumose setae & 1 short naked seta	Free segment with 4 plumose setae & 1 short naked seta	Free segment with 4 plumose setae & a tiny spinule representing fifth seta
Usually wider than long, sometimes longer than wide, rarely more than twice as long; with 7 elements including 1 seta in distal half of ramus	2·0 or more times longer than wide; with 9 elements including 2 lateral setae in proximal half of ramus	Nearly twice as long as wide; with 9 elements including 2 lateral setae in proximal half of ramus	More than twice as long as wide; with 9 elements including 2 lateral setae in proximal half of ramus

mented endopod with distal segment bearing 3 lateral and 7 terminal elements; 4-segmented exopod with 2 setae on segment 1, 1 seta each on segments 2 and 3 and 3 setae on the distal segment. Mandible with unarmed basis and 1-segmented rami; endopod with 3 proximal setae on medial margin and 6 apical setae; exopod with 1 medial margin and 2 apical setae. First maxilla inner lobe armed with 9 elements, outer lobe with 11 elements. Second maxilla with 1 seta on basal segment, claw elongate with 1 plumose seta, a proximal curved row of tiny spinules and a distal row of pinnules. Maxilliped 3-segmented and with a terminal claw; middle segment with

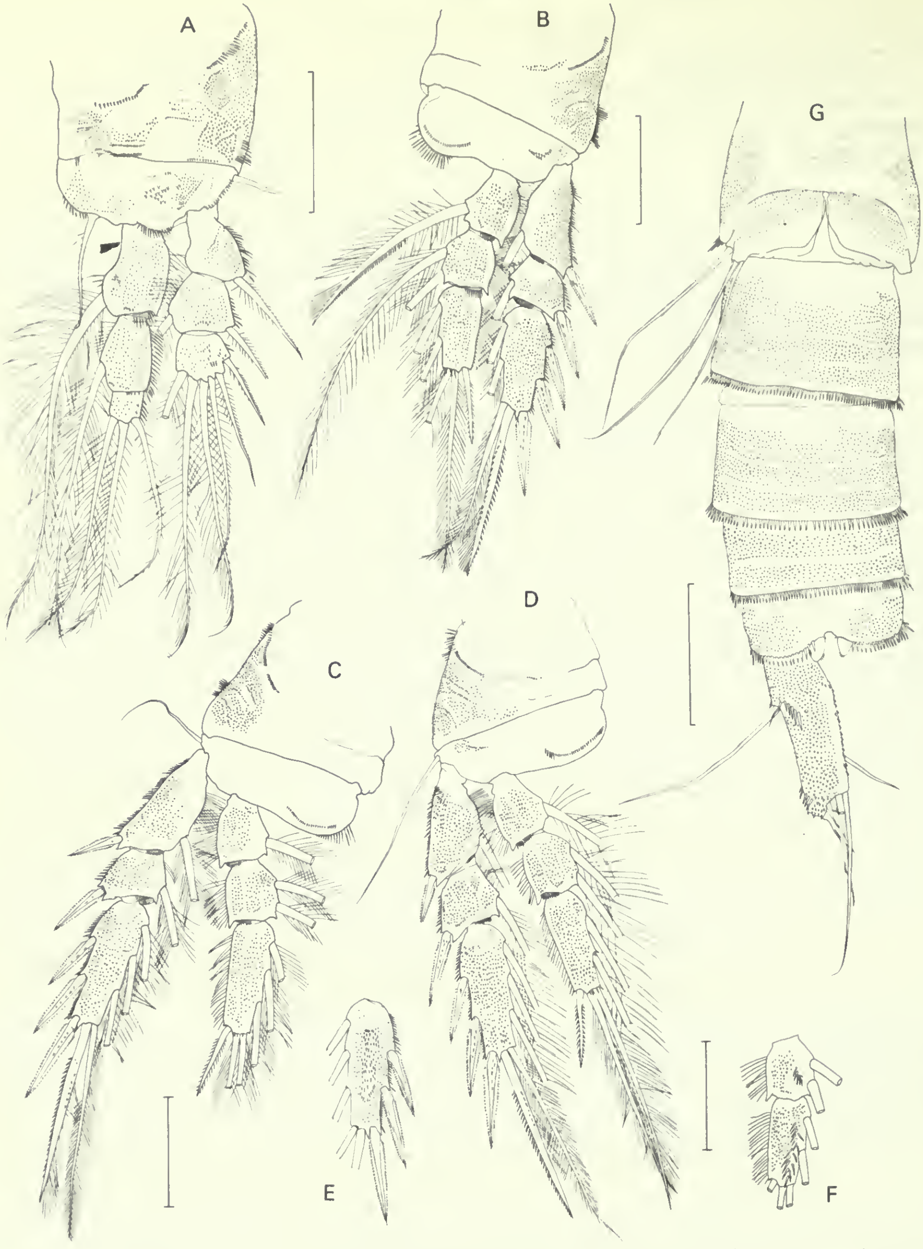

Fig. 5 *Bathyidia remota* male: A, first leg, anterior; B, second leg; C, third leg; D, fourth leg; E, third exopod segment of fourth leg, posterior; F, second and third endopod segments of fourth leg, posterior; G, urosome. Scales 0·1 mm.

setule rows, distal segment with 2 setae; displaying sexual dimorphism with distal segment bearing strong chitinous process in ♂.

Legs 1–4 with 3-segmented rami; armature formula as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1–I	0–1; 0–1; I, 2	I–0; I–1; 6
Leg 2	0–0	1–0	0–1; 0–2; I, 2, 2	I–1; I–1; III, I, 3
Leg 3	0–0	1–0	0–1; 0–2; I, 2, 3	I–1; I–1; III, I, 4
Leg 4	0–0	1–0	0–1; 0–2; I, 2, 2	I–1; I–1; III, I, 4

Leg 1 endopod about 25–30% longer than exopod; inner spine on basis stout and spinulate; spine on outer margin of exopod segment 1 strongly developed, that on segment 2 setiform; endopod segment 3 very small bearing an outer spine, a distal seta and a small inner seta. Leg 2 displaying sexual dimorphism in armature of inner seta of endopod segment 1. Legs 1–4 with very minute denticles on surfaces of coxa, basis and rami; also spinule rows present on posterior surfaces of endopod segments 2 and 3 of legs 2–4.

Leg 5 with small baseoendopod and elongate free segment, ventral surface of latter covered with minute denticles; baseoendopod with outer plumose seta and 3 inner setae in ♀ or 1 in ♂; free segment expanded laterally with short spinules along outer margin; armature comprising 1 lateral seta positioned at apex of lateral expansion, 1 distal seta on inner margin and 2 plumose setae and a small naked seta around apex.

Leg 6 represented by 3 long plumose setae in ♂.

TYPE-SPECIES. *Volkmannia forficula* sp. nov.

ETYMOLOGY. This genus is named after Dr Brigitte Volkmann in recognition of her work on the genus *Tisbe.*

REMARKS. The new genus can be distinguished from *Paraidya*, *Bathyidia*, *Tisbella*, *Neotisbella* gen. nov. and *Tisbintra* by the segmentation of the leg 1 and the armature of the mandibular palp. Although there is a close superficial resemblance between *Volkmannia* and *Tisbe* there are significant differences in the mandible, leg 1 and caudal rami. The mandible of *Tisbe* possesses at least one seta on the basis whereas the mandible of *Volkmannia* has an unarmed basis. The distal segment of the leg 1 endopod in *Tisbe* usually possesses only 2 (occasionally 3) armature elements at least one of which is armed with a distal comb of long setules; similar combs are also found on the outer margin elements of exopod segments 2 and 3 in *Tisbe* species. The distal segment of leg 1 endopod possesses 3 armed elements in *Volkmannia* species, and none of the elements on either ramus is armed with a distal comb of setules. The caudal ramus of *Volkmannia* closely resembles that found in *Bathyidia* and *Neotisbella*, but differs greatly in both structure and armature from that found in *Tisbe.*

Volkmannia forficula sp. nov.

DIAGNOSIS. Prosome rounded, maximum body width about mid-point of prosome (Figs 6A, 8D). Genital complex (♀) and urosome somites 3, 4, 5 and 6 (in ♂) provided with ventral and lateral rows of spinules along posterior borders. Genital area (♀) (Fig. 6F) with a short outer plumose seta and 2 subequal long inner naked setae. Caudal ramus (Fig. 6D) about 2·6 times longer than greatest width; armed with 2 lateral setae in proximal half of ramus (the lateral being about 1·9 times longer than the ventro-lateral one), an oblique spinule row extending from near base of lateral seta, another spinule row around outer distal angle, a naked seta on dorsal surface, a seta at the outer distal angle and 1 at the inner distal angle, 2 long plumose setae on the inner portion of the distal margin and 2 elements in the middle of the distal margin. The latter 2 elements are thin walled and flaccid.

Relative lengths of ♀ first antenna segments 14 : 18 : 20 : 16 : 5 : 8 : 3 : 16 (Fig. 7A); armature elements as follows; segment I–1, II–14, III–7, IV–4+1 aesthete, V–0, VI–4, VII–1, VIII–5; segment I also bearing 2 rows of spinules. First antenna (♂) armature as follows; segment I–1, II–11, III–4, IV–2, V–6+1, aesthete VI–2, VII–2, VIII–2, IX–11 (Fig. 8E); segment I also bearing 2 spinule rows.

Other cephalic appendages as in generic diagnosis (p. 213).

Maxilliped terminal claw with single spinule on concave margin in both sexes (Figs 6E, 8F).

Leg 1 provided with extremely minute denticles on its surface (as in *Bathyidia* and *Neotisbella* but too small to be accurately figured); inner spine on basis strongly developed, much shorter than endopod segment 1 and armed with long pinnules proximally and short pinnules distally (Fig. 7D). Outer margin of exopod segment 1 with well-developed spine, slightly swollen proximally; outer margins of exopod segments 2 and 3 bearing setiform elements armed with short

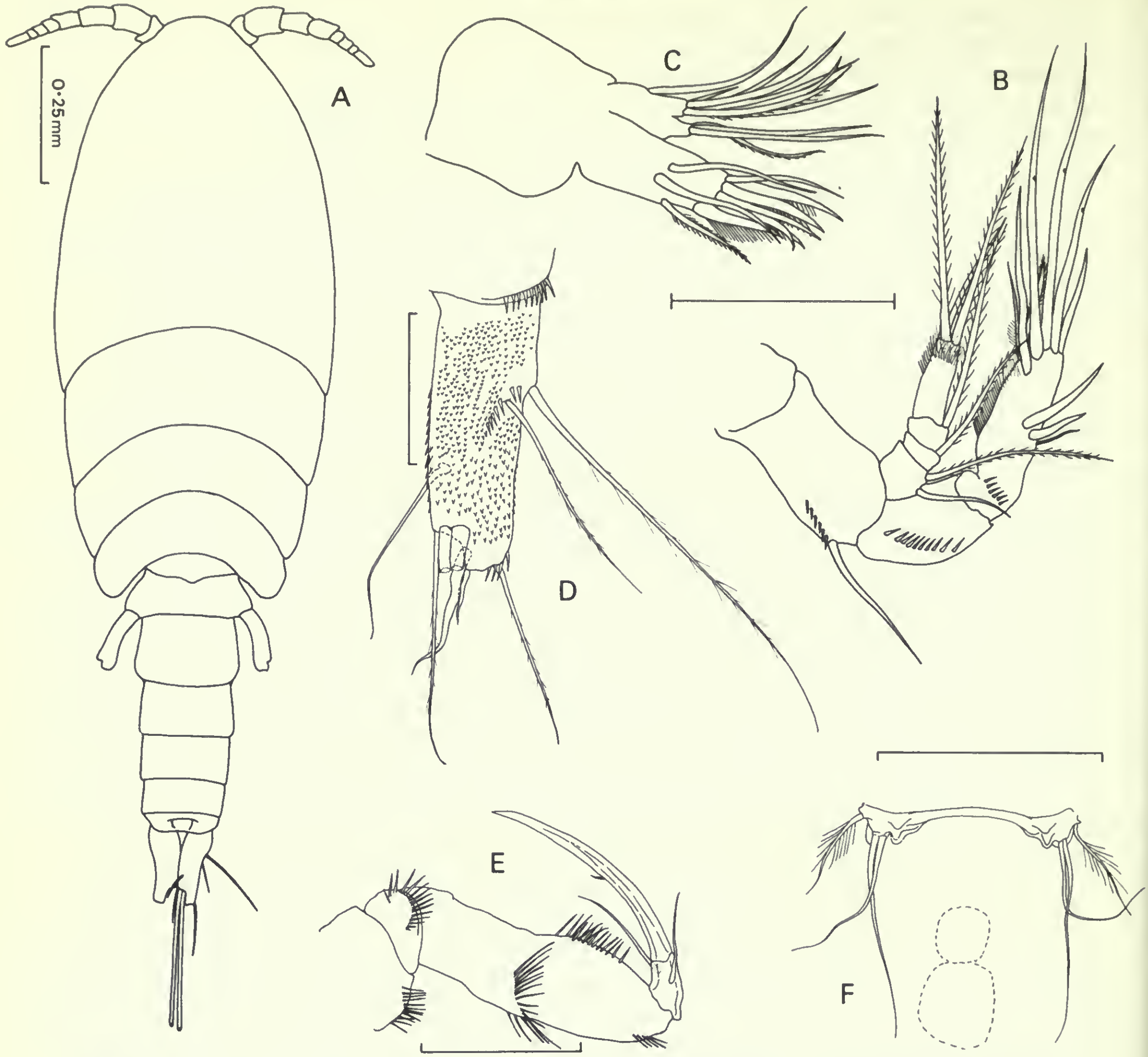

Fig. 6 *Volkmannia forficula* n. sp.: A, female; B, second antenna; C, first maxilla; D, caudal ramus; E, maxilliped; F, genital area. Scales 0·1 mm unless otherwise indicated.

pinnules. Endopod about 34% longer than exopod, relative lengths of endopod segments 56 : 39 : 5; outer element on endopod segment 3 setiform and sparsely provided with short spinules; middle element forked at tip in both sexes (Fig. 7E) and very sparsely pinnate, inner element a short and very slender naked seta.

Legs 2–4 (Figs 8A–C, G) provided with extremely minute denticles on their surfaces as in leg 1; exopod segment 3 with central patch of larger denticles on posterior surface; endopod segments 2 and 3 with some very minute denticles and about 5 and 12–16 spinules respectively on their posterior surfaces (Figs 8A, B). Leg 2 displaying sexual dimorphism, with inner seta on endopod segment 1 armed with an additional row of spinules distally in ♂ (Fig. 8G).

Leg 5 ♀ (Fig. 7F) with endopod represented by 3 setae on baseoendopod, a medium length inner seta with small pinnules, a long middle seta with small pinnules and a small outer naked seta; free segment expanded laterally, about 2·5 times longer than wide; ventral surface covered with irregularly arranged denticles of varying size and bearing a row of short spinules laterally; armature elements comprising 1 medium length plumose seta at the distal angle of the lateral

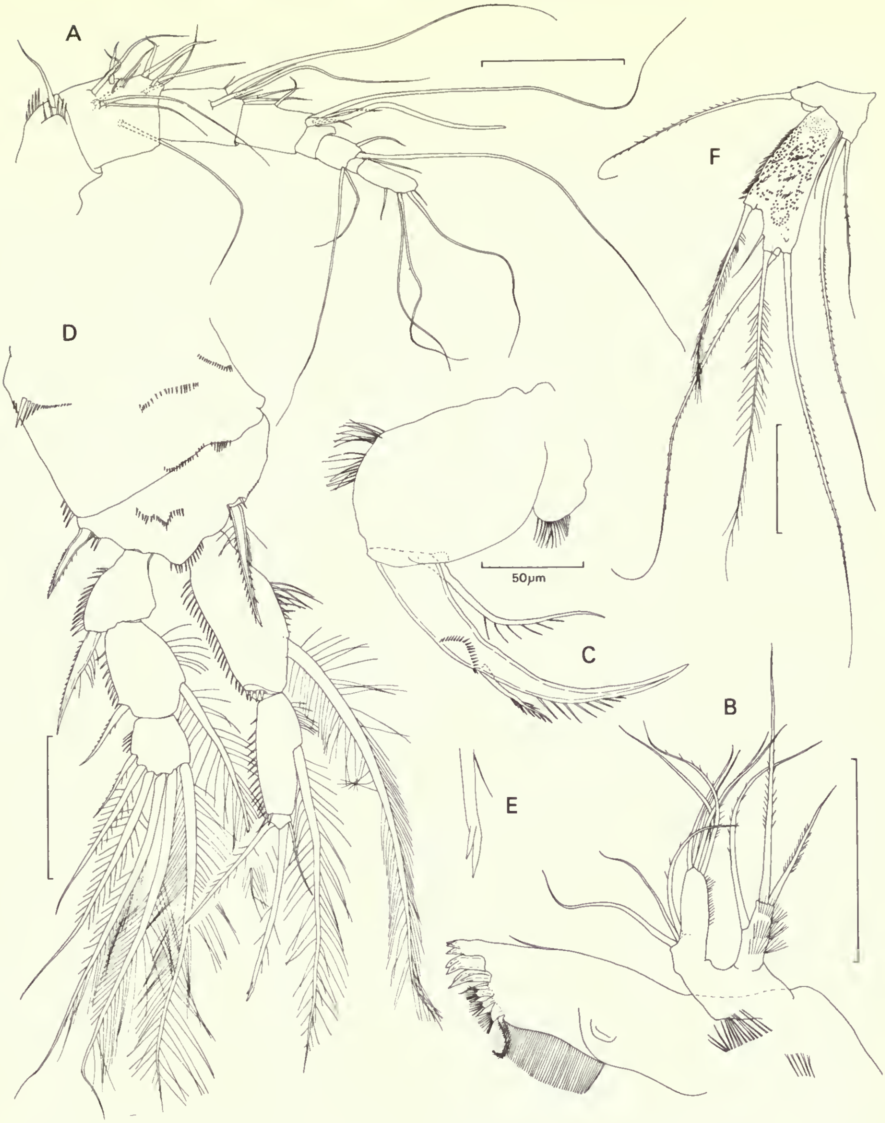

Fig. 7 *Volkmannia forficula* n. sp.: A, female first antenna; B, mandible; C, second maxilla; D, first leg; E, tip of apical seta of third endopod segment of first leg; F, fifth leg. Scales 0·1 mm unless otherwise indicated.

expansion, 1 minutely pinnate long seta at the inner distal angle, 2 long distal setae, the inner minutely pinnate and the outer plumose, and a short naked seta positioned between them and the lateral seta. Leg 5 (♂) as for female except only a single short and minutely pinnate seta present on baseoendopod (Fig. 8H); free segment about 2·3 times longer than greatest width, armature elements similar except the lateral plumose seta is relatively longer than in female.

Leg 6 (♂) comprising 1 medium length sparsely pinnate inner seta and 2 similar but longer outer setae positioned laterally on genital lobes of urosome somite 2 (Fig. 8I).

Body length of ♀♀ from 1·22 to 1·63 mm and ♂♂ from 1·04 to 1·18 mm.

Material examined. Holotype ♀, 2 ♂♂ and 6 ♀♀ paratypes: N.E. Atlantic Ocean 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.233 (holotype), 1977.234–5 (♂♂) and 1977.236–241 (♀♀).

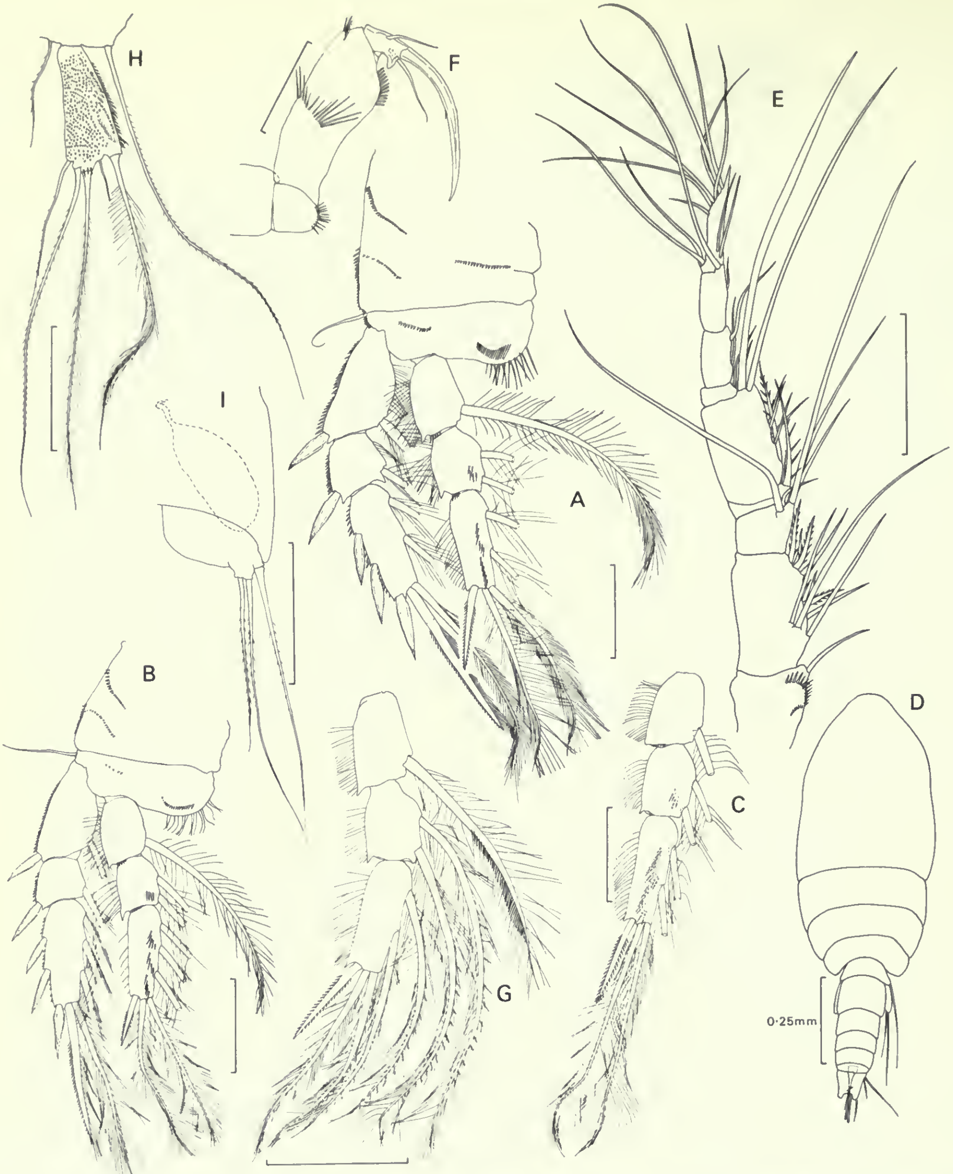

Fig. 8 *Volkmannia forficula* n. sp.: A, female second leg, posterior; B, third leg; C, endopod of fourth leg, anterior; D, male; E, first antenna; F, maxilliped; G, endopod of second leg, anterior; H, fifth leg; I, sixth leg. Scales 0·1 mm unless otherwise indicated.

REMARKS. The general similarity between the males and females described above and the presence of very distinctive characters in both sexes, such as the forked middle seta on the apex of leg 1 endopod, indicate that they are conspecific. Sexual dimorphism was noted in the third maxilliped segment, as in *Bathyidia* and *Neotisbella*, and in the setation of the baseoendopod of leg 5, as in *Neotisbella*.

Volkmannia attenuata sp. nov.

DIAGNOSIS. Prosome very broad (possibly due to distortion), maximum body width about mid-point of prosome (Fig. 9A). Genital complex and urosome somites 3, 4 and 5 provided with spinule

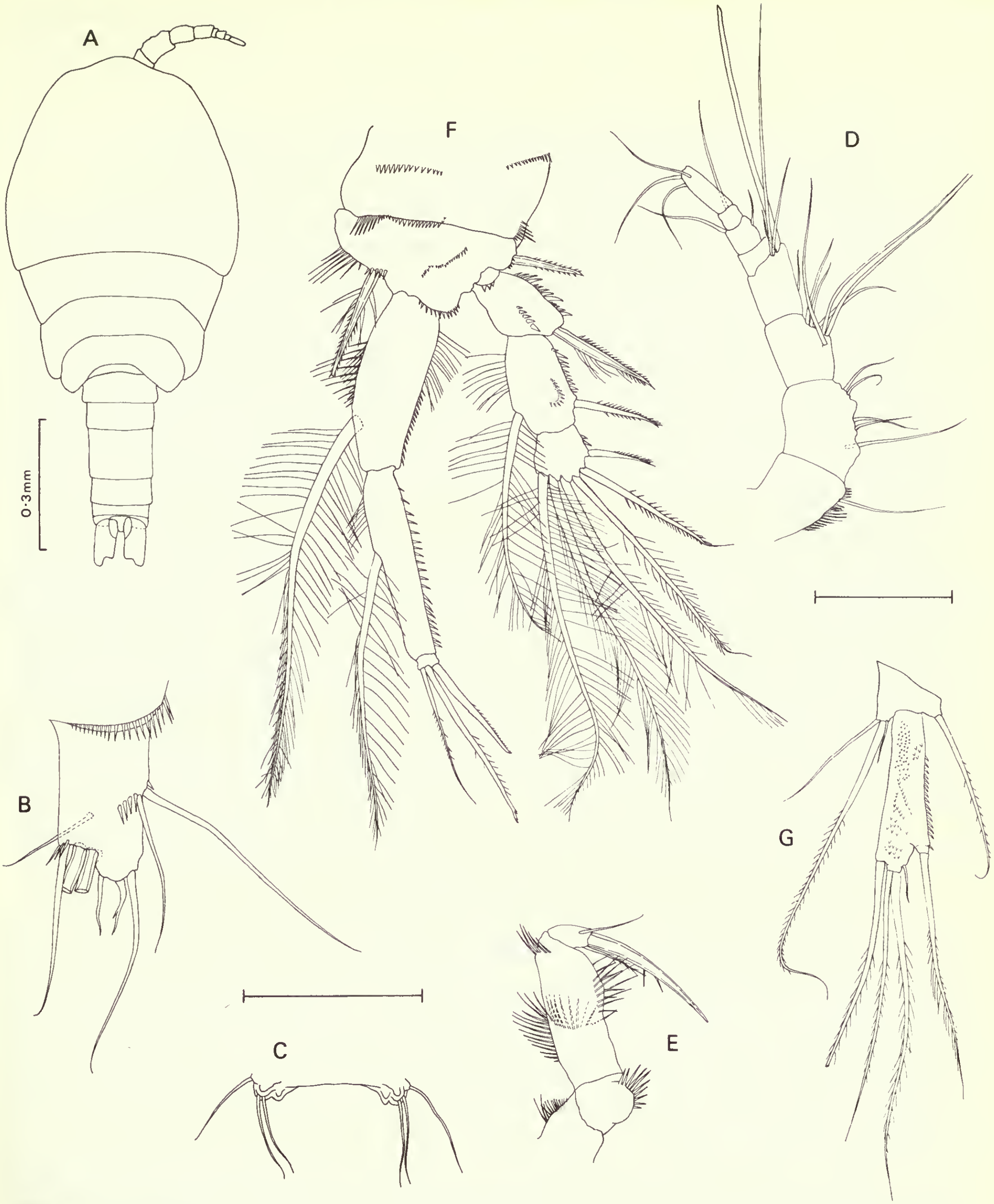

Fig. 9 *Volkmannia attenuata* n. sp., holotype female: A, dorsal; B, caudal ramus; C, genital area; D, first antenna; E, maxilliped; F, first leg; G, fifth leg. Scales 0·1 mm unless otherwise indicated.

rows all around posterior borders except ventrally on somite 3. Genital area (♀) with 3 approximately equal naked setae (Fig. 9C). Caudal ramus (Fig. 9B) about 2 times longer than greatest width; armed with 2 lateral setae in proximal half of ramus (the lateral being about 1·7 times longer than the ventro-lateral one), an oblique spinule row on the ventral surface extending from near base of ventro-lateral seta, some spinules at inner distal angle, a naked seta on dorsal surface, a seta at outer distal angle and 1 at inner distal angle, 2 long plumose setae on inner portion of distal margin and 2 elements on outer portion of distal margin. The latter 2 elements are thin walled and flaccid.

Relative lengths of ♀ first antenna segments 13 : 18 : 19 : 15 : 7 : 8 : 5 : 15 (Fig. 9D); armature incomplete, elements present as follows: segment I–1, II–5, III–6, IV–4+1 aesthete, V–0, VI–2, VII–1, VIII–3; segment 1 also bearing a row of spinules.

Other cephalic appendages as in generic diagnosis (p. 213).

Maxilliped (Fig. 9E) with 5 rows of setules on middle segment; terminal claw with 2 spinules on concave margin.

Leg 1 provided with extremely small surface denticles (too small to be accurately figured); inner spine on basis strongly developed, shorter than endopod segment 1, armed with long pinnules proximally and short pinnules distally (Fig. 9F). Exopod segment 1 with well-developed outer margin spine and a row of 5 broad spinules on anterior surface; outer margins of exopod segments 2 and 3 bearing setiform elements armed with short pinnules. Endopod about 70% longer than exopod, relative lengths of endopod segments 47 : 50 : 3; outer element on endopod segment 3 spiniform and unilaterally provided with short pinnules, middle element subdivided at tip and sparsely pinnate, inner element a slender sparsely pinnate seta.

Legs 2–4 damaged and incomplete but the armature elements appear to be similar to those of *Volkmannia forficula.*

Leg 5 (Fig. 9G) with endopod represented by 3 setae on baseoendopod, a small inner seta, a long middle seta with small pinnules, and a very small outer naked seta; free segment not markedly expanded laterally, about 3·2 times longer than greatest width; ventral surface with irregularly arranged denticles of varying sizes and a row of short spinules laterally; armature elements comprising 1 medium length plumose seta at outer distal angle, 1 pinnate seta (broken in holotype) at the inner distal angle, 2 medium length pinnate setae distally and a short naked seta positioned between them and the lateral seta.

Body length of holotype ♀ 1·18 mm. Male unknown.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean 20° N 21° W, 'Discovery' Stn 9131 18. BM(NH) registration number 1977.324.

REMARKS. This species can be distinguished from *V. forficula* by the elongate endopod of leg 1 (from which the specific name is derived) and by the proportions of the leg 5 and caudal rami.

Genus *NEOTISBELLA* gen. nov.

DIAGNOSIS. Prosome 4-segmented, large and vaulted; urosome 5-segmented in ♀ and 6-segmented in ♂. Dorsal surface of prosome and whole surface of urosome more or less covered with minute denticles. Rostrum small. Genital complex (♀) subdivided by dorsal and dorso-lateral suture line; genital area with 1 long plumose outer seta and 2 short naked inner setae either side of oviduct openings. Caudal rami more than twice as long as wide, with 2 lateral, 1 dorsal and 4 distal setae, plus 2 additional elements on the distal margin.

First antenna 8-segmented (♀) with aesthete on segment 4; 9-segmented (♂) with aesthete on segment 5, geniculate between segments 7 and 8. Second antenna with unarmed basis; 2-segmented endopod, distal segment with 3 lateral and 7 terminal elements; 4-segmented exopod, segments 1 and 3 bearing 1 seta each, segment 2 unarmed and distal segment with 3 seta. Mandible with unarmed basis and 1-segmented rami; endopod with 1 proximal seta on medial margin and 4 apical setae; exopod with 1 medial and 2 apical setae. First maxilla inner lobe armed with 10 elements, outer lobe bearing 11 elements. Second maxilla with 1 seta on basal segment, claw elongate bearing 1 short plumose seta and a distal row of pinnules. Maxilliped comprising 3 segments and a terminal claw; middle segment with 3 rows of setules, distal segment bearing 2 setae; displaying sexual dimorphism with the distal segment bearing a strong chitinous process in ♂.

Leg 1 with 3-segmented exopod and 2-segmented endopod, legs 2–4 with both rami 3-segmented; armature formula as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1–I	0–1; I, 2, 1	I–0; I–1; 6
Leg 2	0–0	1–0	0–1; 0–2; I, 2, 2	I–1; I–1; III, I, 3
Leg 3	1–0	1–0	0–1; 0–2; I, 2, 3	I–1; I–1; III, I, 4
Leg 4	0–0	1–0	0–1; 0–2; I, 2, 2	I–1; I–1; III, I, 4

Leg 1 endopod about 10% longer than exopod; inner spine on basis long and pinnate; spines on outer margins exopod segments 1 and 2 setiform; endopod segment 2 with many slender spinules laterally and distally. Leg 2 displaying sexual dimorphism in structure of inner seta of endopod segment 1. Legs 1–4 with minute denticles on surfaces of coxa, basis and rami; also spinule rows present on posterior surfaces of endopod segments 2 and 3.

Leg 5 comprising small baseoendopod and elongate free segment, ventral surfaces of both covered irregularly with minute denticles; baseoendopod with outer plumose seta and inner plumose seta; free segment with slender spinules all along lateral and ventro-lateral surfaces, and on middle portion of medial surface; armature comprising 1 distal seta on both inner and outer margins and 2 plumose setae and a small naked seta around the apex. Leg 6 represented by 1 short and 2 long plumose setae in ♂.

TYPE-SPECIES. *Neotisbella gigas* sp. nov.

ETYMOLOGY. The generic name alludes to the superficial similarity between the new genus and *Tisbella.*

REMARKS. The only other genera in the subfamily Tisbinae which possess a 2-segmented endopod on the leg 1 are *Tisbella* and *Tisbintra.*

The reduction in the number of armature elements on leg 1 endopod serves to separate *Tisbintra* from both *Tisbella* and the new genus. Some of the significant differences between *Tisbella* and *Neotisbella* are tabulated in Table 2. Other differences are the relative size of the endopod segments of legs 2–4, and the presence of an outer spine on exopod segment 2 of the leg 1 in *Tisbella* compared with the setiform element present in *Neotisbella.*

Neotisbella gigas sp. nov.

DIAGNOSIS. Prosome angular and vaulted in appearance (Fig. 10A); maximum width in anterior third of cephalosome (Fig. 12A). Genital complex (♀) and urosome somites 3, 4, 5 and 6 (in ♂) provided with ventral and lateral rows of spinules along posterior borders. Genital area (♀) (Fig. 11G) with a short inner naked seta, a slightly longer naked middle seta and a long plumose lateral seta. Caudal ramus (Fig. 10F) about 1·9 times longer than greatest width; armed with 2 lateral setae in proximal half of ramus (the lateral being about 1·7 times longer than the ventro-lateral one), an oblique spinule row on ventral surface extending from near base of lateral seta, a spinule row just proximal to the distal margin, a naked seta on the dorsal surface, a seta at the outer distal angle and one at the inner distal angle, 2 medium length plumose setae on the inner portion of the distal margin and 2 elements in the middle of the distal margin. The latter 2 elements are thin-walled and bifurcated at different levels.

Relative lengths of ♀ first antenna segments 9 : 19 : 19 : 17 : 9 : 10 : 4 : 13 (Fig. 10B); armature elements as follows; segment I–1, II–13, III–9, IV–3+1 aesthete, V–2, VI–5, VII–1, VIII–5; all segments provided with minute denticles on surfaces and segment I bearing large area of spinules, segment III about 6 spinules and segment IV 3 irregular rows of spinules. First antenna (♂) armature elements as follows; segment I–1, II–15, III–8, IV–2, V–8+1 aesthete, VI–2, VII–2, VIII–0 (?), IX–11 (Fig. 12B); segment I with 2 spinule rows, segment 7 with several rows of short spinules on antero-ventral surface (see Fig. 12C).

Other cephalic appendages as in generic diagnosis (p. 222).

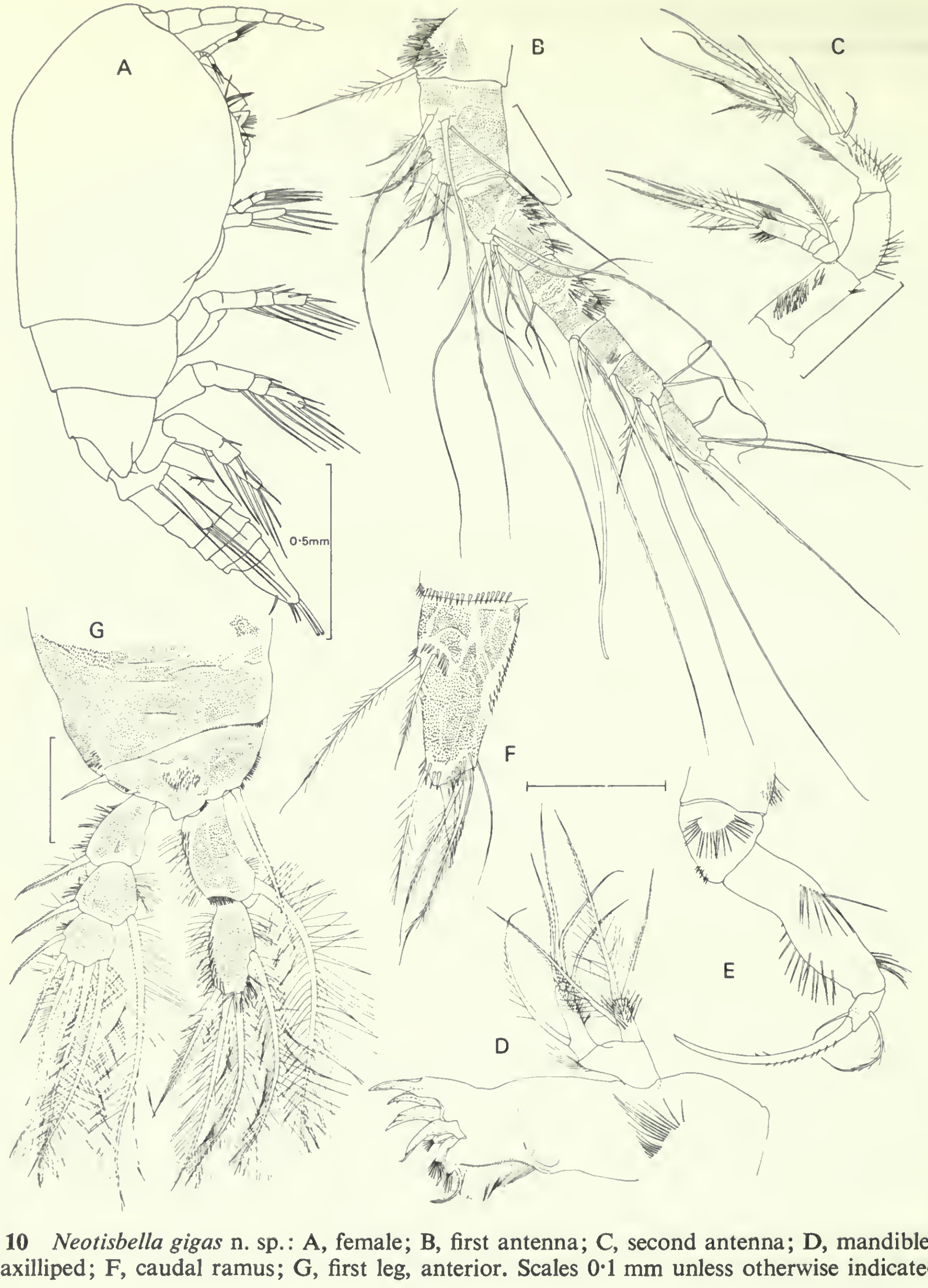

Fig. 10 *Neotisbella gigas* n. sp.: A, female; B, first antenna; C, second antenna; D, mandible; E, maxilliped; F, caudal ramus; G, first leg, anterior. Scales 0·1 mm unless otherwise indicated.

Maxilliped terminal claw bearing a row of outer spinules on the convex margin in both sexes and two spinules on concave margin in ♀ (Fig. 10E); one spinule in ♂ (Fig. 12D).

Inner spine on basis of leg 1 much longer than endopod segment 1 and armed with small pinnules in ♀ (Fig. 10G); shorter than segment 1 and apparently naked in ♂ (Fig. 12E). Armature elements on outer margins of exopod segments all setiform, those on segments 1 and 2 and the 3 proximal elements on segment 3 with shorter pinules than those on distal margin of segment 3; outer element on endopod segment 2 setiform but armed with shorter pinnules than the outer

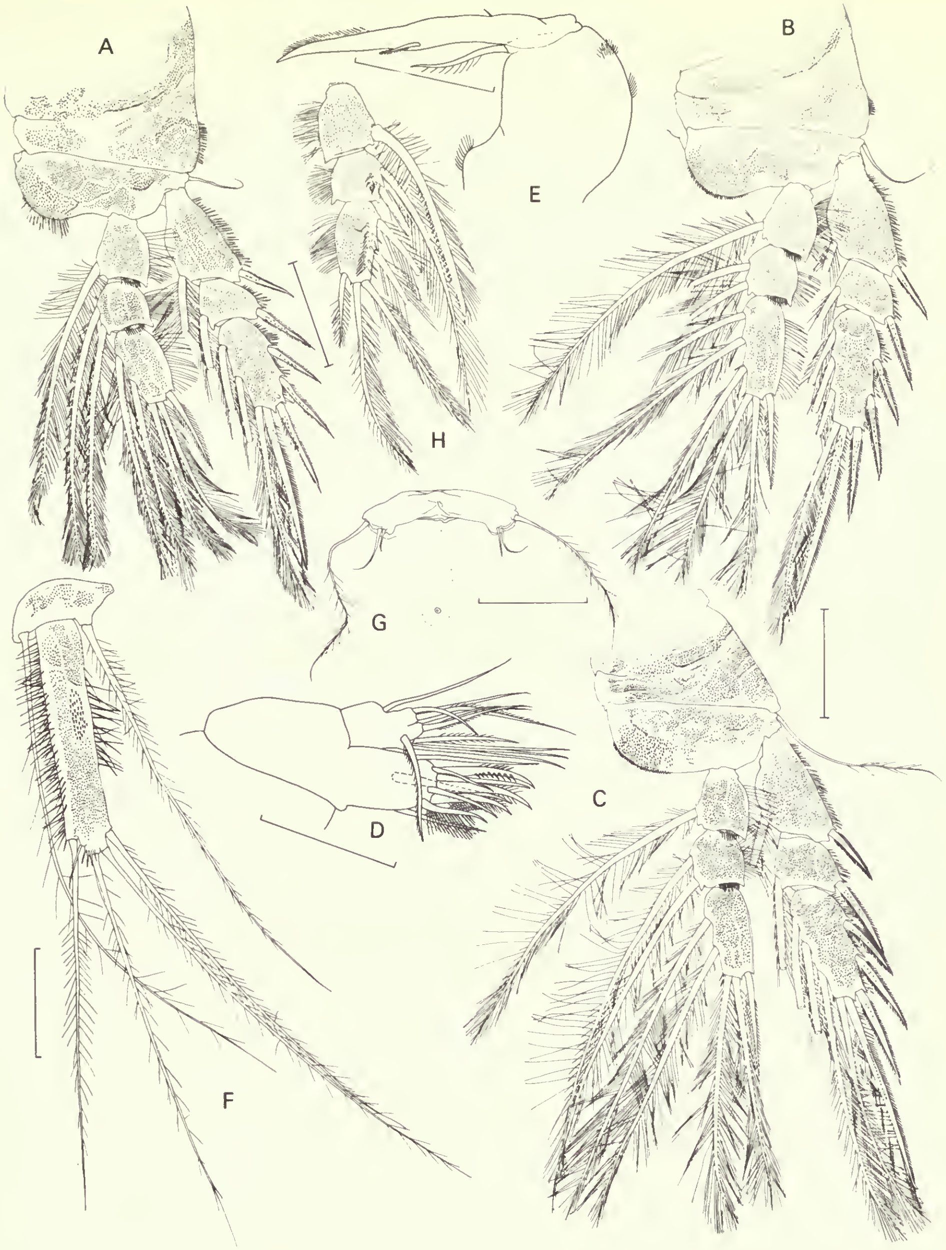

Fig. 11 *Neotisbella gigas* n. sp.: A, second leg, anterior; B, third leg; C, fourth leg; D, first maxilla; E, second maxilla; F, fifth leg; G, genital area; H, male endopod of second leg, posterior. Scales 0·1 mm.

two distal plumose setae; endopod segments 1 and 2 both with long spinules on lateral and disto-medial surfaces.

Legs 2–4 (Figs 11A–C); exopod segment 3 bearing central patch of larger denticles on posterior surface; endopod segments 2 and 3 armed with some denticles and about 7 and 16 spinules respectively on their posterior surfaces (Fig. 11H). Leg 2 displaying sexual dimorphism, the inner seta on endopod segment 1 stout and spiniform, and armed with distal row of stout spinules (Fig. 11H).

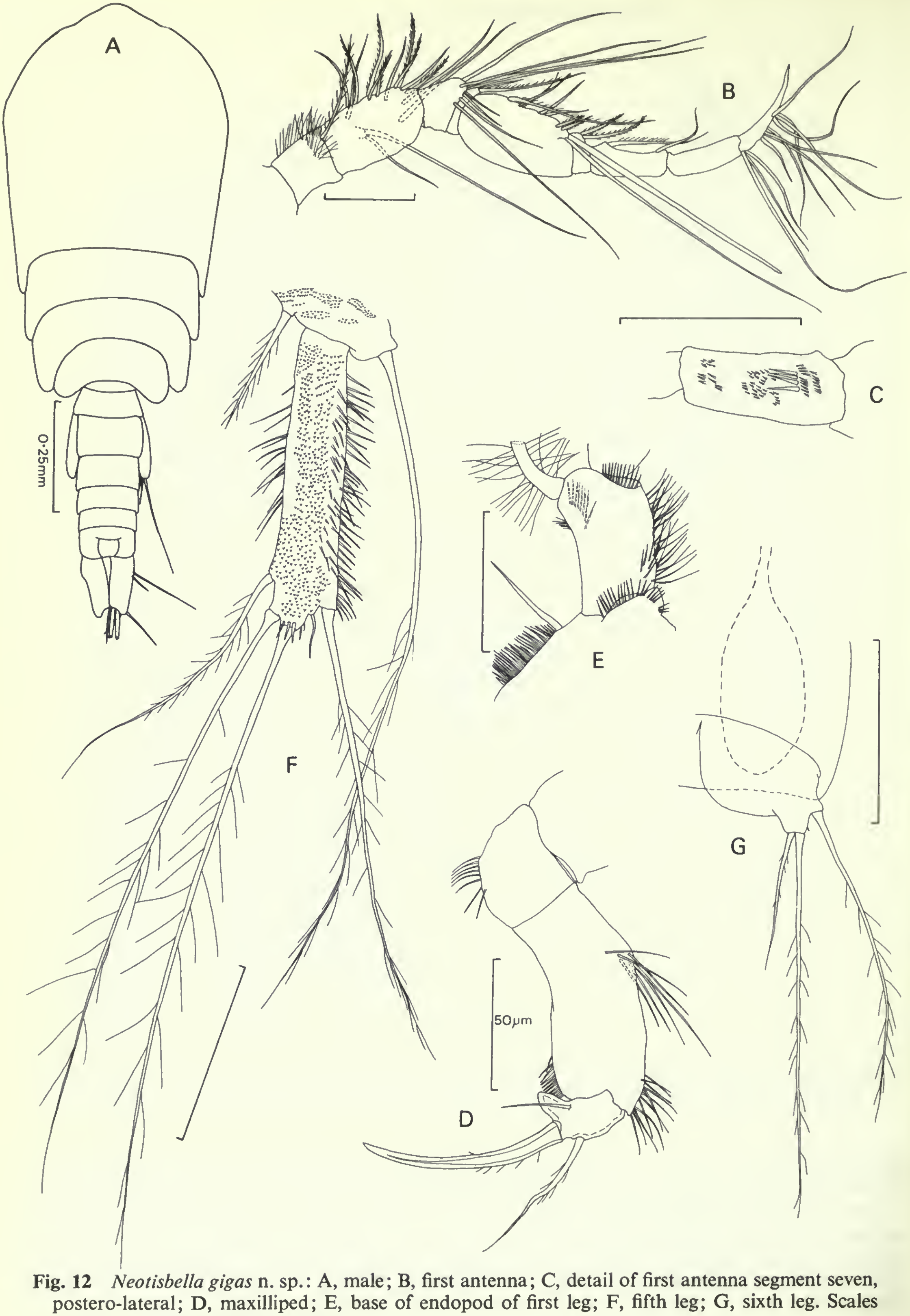

Fig. 12 *Neotisbella gigas* n. sp.: A, male; B, first antenna; C, detail of first antenna segment seven, postero-lateral; D, maxilliped; E, base of endopod of first leg; F, fifth leg; G, sixth leg. Scales 0·1 mm unless otherwise indicated.

Leg 5 ♀ (Fig. 11F) with single inner seta on baseoendopod about twice as long as free segment: free segment about 5·3 times longer than wide; its ventral surface covered with minute denticles; its lateral surface and the middle third of the medial surface bearing many spinules; armature elements comprising 1 long plumose seta each at the distal ends of the lateral and medial margins, 2 long plumose setae on the projecting distal margin and a short naked seta positioned between them and the lateral seta. Leg 5 in ♂ (Fig. 12F) as for female except inner seta on baseoendopod about half as long as free segment.

Leg 6 of ♂ (Fig. 12G) comprising 1 short sparsely pinnate inner seta and 2 long sparsely pinnate outer setae situated laterally on genital lobes of urosome somite 2.

Body length of ♀♀ from 1·85 to 2·00 and ♂ 1·26 mm.

MATERIAL EXAMINED. Holotype ♀, 1 ♂ and 5 ♀♀ paratypes: N.E. Atlantic Ocean, 18° N 25° W 'Discovery' Stn 7089. BM(NH) registration numbers 1977.226 (holotype), 1977.227 (♂) and 1977.228–232 (♀♀).

REMARKS. The similarities between the male and females described above strongly suggest that they are conspecific. Apart from the obvious characters of urosome segmentation, structure of the first antenna and the leg 6, differences between the sexes were noted in the maxilliped, leg 1 and leg 5. The presence of a spinous process on the third maxilliped segment has been recorded in males of *Bathyidia remota* and *Volkmannia forficula*. The minor differences between the sexes in the inner spine on the basis of the leg 1 and the inner seta on the baseoendopod of leg 5 can readily be attributed to sexual dimorphism.

Phylogenetic relationships of the new genera

It is interesting to examine the possible phylogenetic relationships of the two new genera, *Volkmannia* and *Neotisbella*, to other genera in the family Tisbidae. The new genera belong to the subfamily Tisbinae which contains the following genera: *Tisbe*, *Tisbella*, *Tisbintra*, *Bathyidia*, *Paraidya*, *Scutellidium* Claus, 1866 and *Sacodiscus* Wilson, 1924. The aberrant genus *Cholidya* Farran, 1914 is profoundly modified for its parasitic mode of life and is here regarded as representing a separate subfamily, the *Cholidyinae* subfam. nov. *Scutellidium* and *Sacodiscus* are closely related and will be called the *Scutellidium* group of genera, all other genera will be referred to as the *Tisbe* group. These two groups of genera are distinguished primarily by the structure of the mouthparts.

Within the *Tisbe* group the main characters used for separating the genera are the structure and armature of the second antenna, mandible, leg 1 and caudal ramus. Consideration of these characters within a phylogenetic framework suggested the following scheme of affinities (Fig. 13).

The main events occurring during the evolutionary radiation of this group of genera are designated, A, B and C (in Fig. 13). Event A resulted in the divergence of the ancestral stock into two lines, the VB lineage (*Volkmannia–Bathyidia*) and the TP lineage (*Tisbe–Paraidya*). Event A was the adoption of a planktonic habit by the VB lineage and the retention of the ancestral benthic habit by the TP lineage. The change to a planktonic existence appears to be associated with the acquisition of an elongate caudal ramus armed with 9 armature elements, as possessed by all 3 genera in the VB lineage. The benthic TP lineage typically possess a short caudal ramus bearing only 6 or 7 armature elements. The second major event (B) seems to have occurred twice, once in each main lineage. This was the divergence from an ancestral stock with a leg 1 endopod comprising three large segments of a stock with a reduced third endopod segment. The genera *Bathyidia* and *Paraidya* both retained large third segments on their leg 1 endopods. The third major event (C) was the splitting off from an ancestral stock possessing a reduced third segment on the leg 1 endopod of a stock in which the separate third segment is lost altogether. This appears to have taken place at least twice, probably three times; once in the derivation of the *Neotisbella* line from the ancestral *Volkmannia* stock and probably twice in the independent separation of the *Tisbella* and *Tisbintra* lines from the ancestral *Tisbe* stock.

This scheme of phylogenetic relationships allows for the obvious close relationship of *Volkmannia*, *Neotisbella* and *Bathyidia* (as indicated by their shared derived characters) despite their

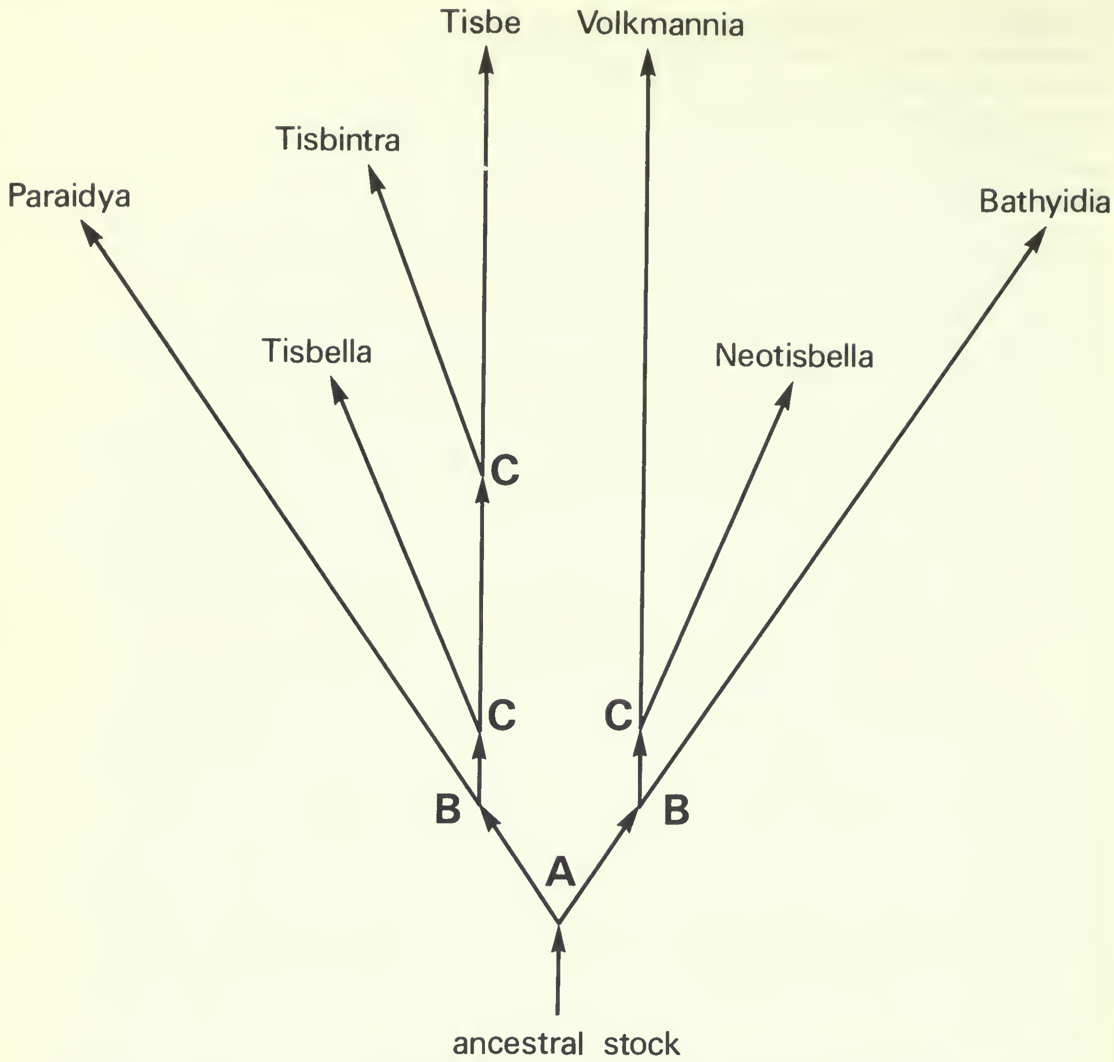

Fig. 13 The affinities of the seven genera of the *Tisbe* group within the subfamily Tisbinae.

close phenetic similarities to *Tisbe*, *Tisbella* and *Paraidya* respectively. The progressive reduction of the third segment of the leg 1 endopod has resulted in the formation of a 2-segmented endopod independently in *Neotisbella*, in *Tisbella* and in *Tisbintra*. In the first two genera the endopod is relatively short and the distal endopod segment retains the combined armature elements of both second (the single inner seta) and third segments (the 3 distal elements). This condition could have been derived from an endopod similar to that found in *Bathyidia* and *Paraidya*. In *Tisbintra* the endopod is much longer than the exopod and the distal endopod segment possesses 1 inner seta and only 1 or 2 distal elements. This condition was probably derived from a more *Tisbe*-like stock.

Family TACHIDIIDAE

Genus *EUTERPINA* Norman, 1903

DIAGNOSIS. As for type-species.

TYPE-SPECIES. *Euterpina acutifrons* (Dana, 1848).

Euterpina acutifrons (Dana, 1848)

Harpacticus acutifrons Dana, 1848 : 153.
Euterpe gracilis Claus, 1863 : 110, pl. XIV, figs 1–13.

Diagnosis. Prosome 4-segmented, first thoracic somite fused to head; urosome 5-segmented in ♀ (Fig. 14G) and 6-segmented in ♂. Genital complex (♀) without subdividing suture line. Rostrum well developed, anteriorly directed. Caudal rami just longer than wide. First antenna (♀) 7-segmented (Fig. 14H) with 2 terminal aesthetes; (♂) indistinctly 5-segmented, chirocerate and with 2 aesthetes on claw-like distal segment (Fig. 14K). Second antenna (Fig. 14I) with basis bearing 1-segmented exopod and 2-segmented endopod. Mandible with poorly developed biramous palp, without setae on basis. First maxilla arthrite well developed with about 12 mostly spiniform armature elements, rami rudimentary. Second maxilla with well-developed basis and small 2-segmented endopod. Maxilliped slender, 3-segmented; the long terminal claw armed with several strong setules. Rami of leg 1 short and 2-segmented, displaying weak sexual dimorphism with the rami being longer and more slender in ♂ (Fig. 14L) than in ♀. Legs 2–4 usually with 3-segmented rami, endopod of leg 2 in ♂ sometimes displaying incomplete separation of segments 2 and 3 giving 2-segmented appearance; armature formula as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	0–I	0–1; I, I, 4	I–0; III, 2, 2
Leg 2	0–0	0–0	0–1; 0–2; I, 2, 2	I–1; I–1; II, I, 3
Leg 3	0–0	0–0	0–1; 0–2; I, 2, 2	I–1; I–1; II, I, 3
Leg 4	0–0	0–0	0–1; 0–1; I, 2, 2	I–1; I–1; II, I, 2

Leg 5 (♀) a flattened plate armed with 4 distal margin spines and 2 elements on the outer margin; a proximal seta, a short spine in the middle of the margin and a fine setule originating in the axil of this spine (Fig. 14J). Leg 5 (♂) with both legs fused into a single plate with a median notch in the distal margin, each leg bearing 2 distal margin spines and 3 elements on the outer margin, a proximal seta, a short spine in the middle of the margin and a fine setule originating in the axil of the spine (Fig. 14M).

Leg 6 (Fig. 14N) in ♂ a small prominence bearing 2 serrate spines apically.

Body lengths of ♀ 0·50–0·75 mm and ♂ 0·50–0·56 mm.

Material examined. 1 ♀: Antarctic, 'Terra Nova' Expedition (Farran, 1929). BM(NH) registration numbers 1930.1.1.1569–70. 4 ♀♀: Cheshire coast. BM(NH) registration numbers 1945.10.29. 21–23. 10 ♀♀, 1 ♂: Starcross, Devon. BM(NH) registration numbers 1911.11.8.43189–198.

Remarks. Both sexes of this species are easily recognizable and are rarely confused with other species. The fine lateral setule present in the axil of the outer margin spine on leg 5 has been reported previously in both the male (e.g. Klie, 1913; Haq, 1965) and the female (e.g. Giesbrecht, 1892; Mori, 1964; Haq, 1965). This setule is not illustrated in either sex by Sars (1921) or in the male by Chappuis (1936) and Giesbrecht (1892). It is probable that the setule has been overlooked by the latter group of authors. It was even found to be present in both morphs of male *E. acutifrons* studied by Haq (1965).

Family **THALESTRIDAE**

Genus *PARATHALESTRIS* Brady and Robertson, 1873

Diagnosis. Prosome 4-segmented, urosome 5-segmented in ♀ and 6-segmented in ♂. Body cylindrical or slightly laterally compressed; epimeral plates of free thoracic somites not markedly produced. Rostrum short, antero-ventrally directed.

First antenna (♀) 7- to 9-segmented, without plumose setae. Second antenna with allobasis and 2-segmented exopod. Mandible palp well developed; basis with 3 setae, both rami 1-segmented. First maxilla with 1-segmented exopod and endopod. Second maxilla with 3 endites on coxa, endopod rudimentary. Maxilliped with 2 robust basal segments and strong terminal claw.

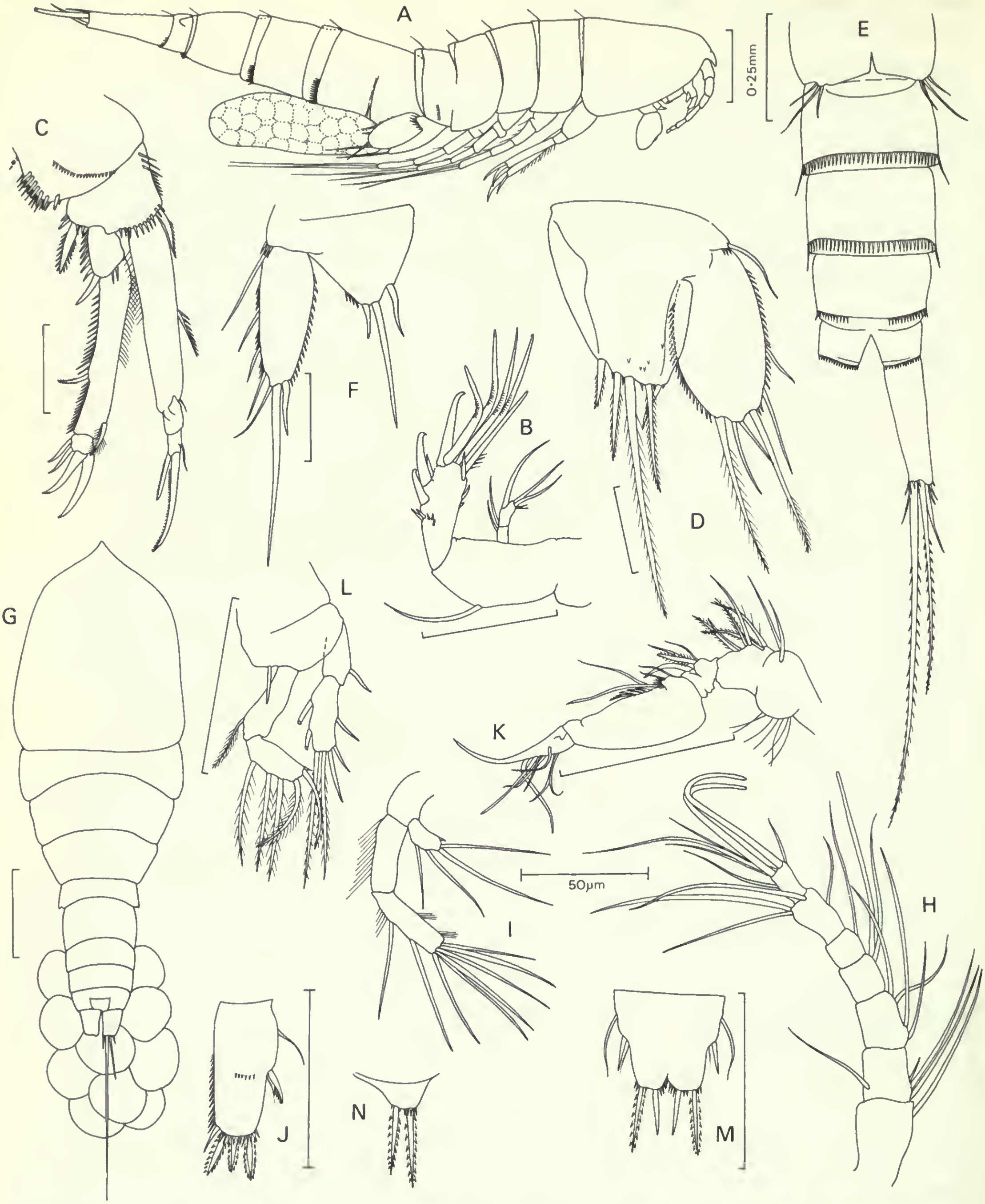

Fig. 14 *Parathalestris croni*: A, female; B, second antenna; C, first leg; D, fifth leg; E, male urosome; F, fifth leg. *Euterpina acutifrons*: G, female; H, first antenna; I, second antenna; J, fifth leg; K, male first antenna; L, first leg; M, fifth leg; N, sixth leg. Scales 0·1 mm unless otherwise indicated.

Leg 1 with both rami 3-segmented, about equal in length; exopod segment 2 and endopod segment 1 providing most of length of respective rami. Legs 2–4 with 3 segmented rami in ♀; leg 2 displaying sex dimorphism, with endopod usually 2-segmented in ♂. Armature formula as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1–I	0–1; 0–0; 3 or 2	I–0; I–1; 4 or 5
Leg 2	0–0	1–0	0–1; 0–2; I, 2, 2	I–1; I–1; II, I, 4
Leg 3	0–0	1–0	0–1; 0–1; I, 2, 3	I–1; I–1; II, I, 5
Leg 4	0–0	1–0	0–1; 0–1; I, 2, 2	I–1; I–1; II, I, 5

Leg 5 ♀ baseoendopod strongly projecting and usually bearing 5 setae, exopod usually with 6 or 7 setae. Leg 5 ♂ usually with 3 setae on baseoendopod and 6 or 7 on exopod.

Leg 6 in ♂ represented by 3 setae on genital lobes of urosome somite 2.

TYPE-SPECIES. *Parathalestris clausi* (Norman, 1868).

REMARKS. Sars (1905) erected a new genus, *Halithalestris*, to include the species *Harpacticus croni*, first recorded by Kroyer (1842). One of the major characters used by Sars to establish the new genus was the pelagic habits of *H. croni*. Lang (1948) recognized that *Halithalestris* was not a distinct genus and subsequently referred *H. croni* to *Parathalestris*.

Parathalestris croni (Kroyer, 1842)

Harpacticus croni Kroyer, 1842: pl. XLIII, figs 3a–n.
Thalestris serrulata Brady, 1880: 133, pl. LIX, figs 2–11.
Halithalestris croni Sars, 1905: 118, pl. LXXII.

DIAGNOSIS. Cephalosome small, comprising about 50% of length of prosome (Fig. 14A); genital complex in ♀ only subdivided laterally by a suture line. Anal somite markedly notched in middle of posterior border (Fig. 14E). Caudal rami divergent, about 3·5–4 times longer than maximum width.

First antenna of ♀ 9-segmented, bearing a large aesthete on segment 4; ♂ indistinctly 7-segmented with aesthetes on segments 3 and 4. Second antenna (Fig. 14B) with 1 seta on allobasis; exopod segments 1 and 2 with 1 and 4 setae respectively. First segment of maxilliped with 3 distal setae, terminal claw shorter than second segment.

Both rami of leg 1 (Fig. 14C) similar in length; inner claw on distal segment of endopod about 2 times longer than outer claw; exopod segment 3 with 4 armature elements. Leg 5 (♀) extending posteriorly as far as middle of genital complex; baseoendopod armed with 5 setae and extending just beyond mid-point of exopod; exopod oval in outline, about twice as long as wide and armed with 6 setae (Fig. 14D). Leg 5 (♂) smaller than in ♀, baseoendopod with 3 setae and exopod with 6 setae (Fig. 14F). Leg 6 in ♂ represented by 3 setae on lateral lobe of urosome 2 (Fig. 14E).

Body length of ♀ from 2·1 to 2·3 mm and ♂ about 1·7 mm.

MATERIAL EXAMINED. 1 ♀, 1 ♂; Firth of Forth. BM(NH) registration numbers 1911.11.8.46207–10.

REMARKS. This is one of the largest species of harpacticoid and is easily distinguished by its size, small cephalosome and long divergent caudal rami. Brady (1880) first described the male, as *Thalestris serrulata*, and figured the male leg 5. Wells (1970) misinterpreted Brady's figure when he redrew the leg 5, as he illustrated only 5 setae on the exopod (Wells, 1970: fig. 7e ♂) instead of the 6 in Brady's figure.

Family **CLYTEMNESTRIDAE**

Genus ***CLYTEMNESTRA*** Dana, 1848

DIAGNOSIS. Prosome 4-segmented, first thoracic somite fused to head, urosome 5-segmented in ♀, 6-segmented in ♂; body rather dorso-ventrally flattened, cephalosome and free thoracic somites with large, conspicuous epimeral plates. Urosome slender; genital complex without subdividing suture line. Rostrum large, anteriorly directed. Caudal ramus at least as long as wide, with 6 armature elements, 2 of which are long in ♂.

First antenna 7- or 8-segmented, with several aesthetes. Second antenna comprising a basis, a 2-segmented endopod and either 1 or 2 plumose setae representing the exopod (Fig. 15F). Mandible reduced to slender blade and palp represented by single minute setule. First maxilla 2-segmented, proximal segment with 1 lateral seta, distal segment with 2 apical elements. Second maxilla reduced, 2-segmented, bearing 1 proximal seta and a distal endite armed with 2 setae on first segment and 3 setae on second segment. Maxilliped long, consisting of 2 segments and a terminal claw; showing weak sexual dimorphism with longer terminal claw in ♂ (Fig. 15G) than in ♀ (Fig. 15D).

Leg 1 with 3-segmented endopod and 1-segmented exopod. Legs 2–4 each with transversely elongate basis and 3-segmented rami: armature formula variable on legs 1 and 2 between species but within following limits:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	0/1–0	0–1; 0–1; 0, 2, 2	3/4
Leg 2	0–0	1–0	0–1; 0–2; I, 2, 2	0/I–1; I–1; II, 2, 2/3
Leg 3	0–0	1–0	0–1; 0–2; I, 2, 3	I–1; I–1; III, 2, 3
Leg 4	0–0	1–0	0–1; 0–2; I, 2, 2	I–1; I–1; III, 2, 3

Leg 5 without inner setae on baseoendopod; free segment elongate with 5 or 6 slender setae. Leg 6 in ♂ represented by an elongate lobe bearing 1 lateral and 2 apical setae.

TYPE-SPECIES. *Clytemnestra scutellata* Dana, 1848.

REMARKS. Lang (1948) in his monograph on the Harpacticoida retained Poppe's (1891) family-group name, Pseudopeltiidae, for the genus *Clytemnestra* which was its type and only genus. This action has been followed by several subsequent authors (e.g. Wells, 1970) but it contravenes the ICZN Article 11e as a family-group name must, when first published, be based on the name then valid for a contained genus. Thus the family-group name Clytemnestridae, first proposed by Scott (1909), is adopted here.

Clytemnestra scutellata Dana, 1848

Goniopelte gracilis Claus, 1891 : 151, pl. I–II.
Clytemnestra hendorffi Poppe, 1891 : 132, pl. I.

DIAGNOSIS. Caudal rami (Figs 15B, J) about 1·8 times longer than greatest width. First antenna 8-segmented; ♀ with 1 aesthete on segment 4 and 2 each on segments 5 and 8; relative lengths of segments 3 : 10 : 10 : 10 : 12 : 10 : 15 : 30 (Fig. 15C); ♂ with 2 aesthetes each on segments 4, 5 and 8; relative lengths of segments 3 : 7 : 14 : 3 : 28 : 5 : 16 : 24 (Fig. 15E). Exopod of second antenna (Fig. 15F) represented by 2 plumose setae. Basis of leg 1 (Fig. 15H) with outer margin seta; exopod with 4 distal setae. Leg 2 (Fig. 15I) exopod segment 1 without outer margin spine; endopod segment 1 of legs 2–4 as long as exopod segments 1 and 2 combined. Free segment of leg 5 typically with 6 setae in both sexes (Fig. 15K), occasionally with 5 (var. *quinquespinosa*).

Body length of ♀ from 1 to 1·24 mm, and of ♂ from 1·07 to 1·3 mm.

MATERIAL EXAMINED. 1 ♀, 1 ♂: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.194 (♀) and 1977.195 (♂). 1 ♀, 1 ♂: Suez Canal Expedition (Gurney, 1927). BM(NH) registration number 1928.4.2.136. 10 ♀♀, 2 ♂♂: as *C. rostrata*, Gulf of Guinea (Scott, 1894). BM(NH) registration numbers 1893.4.22.268–275.

REMARKS. This species can be distinguished from *C. rostrata*, the only other species in the genus, by the shape of the caudal rami and the segmentation of the first antenna when sorting undissected specimens. There are other significant differences between the two species, particularly in the armature of legs 1 and 2.

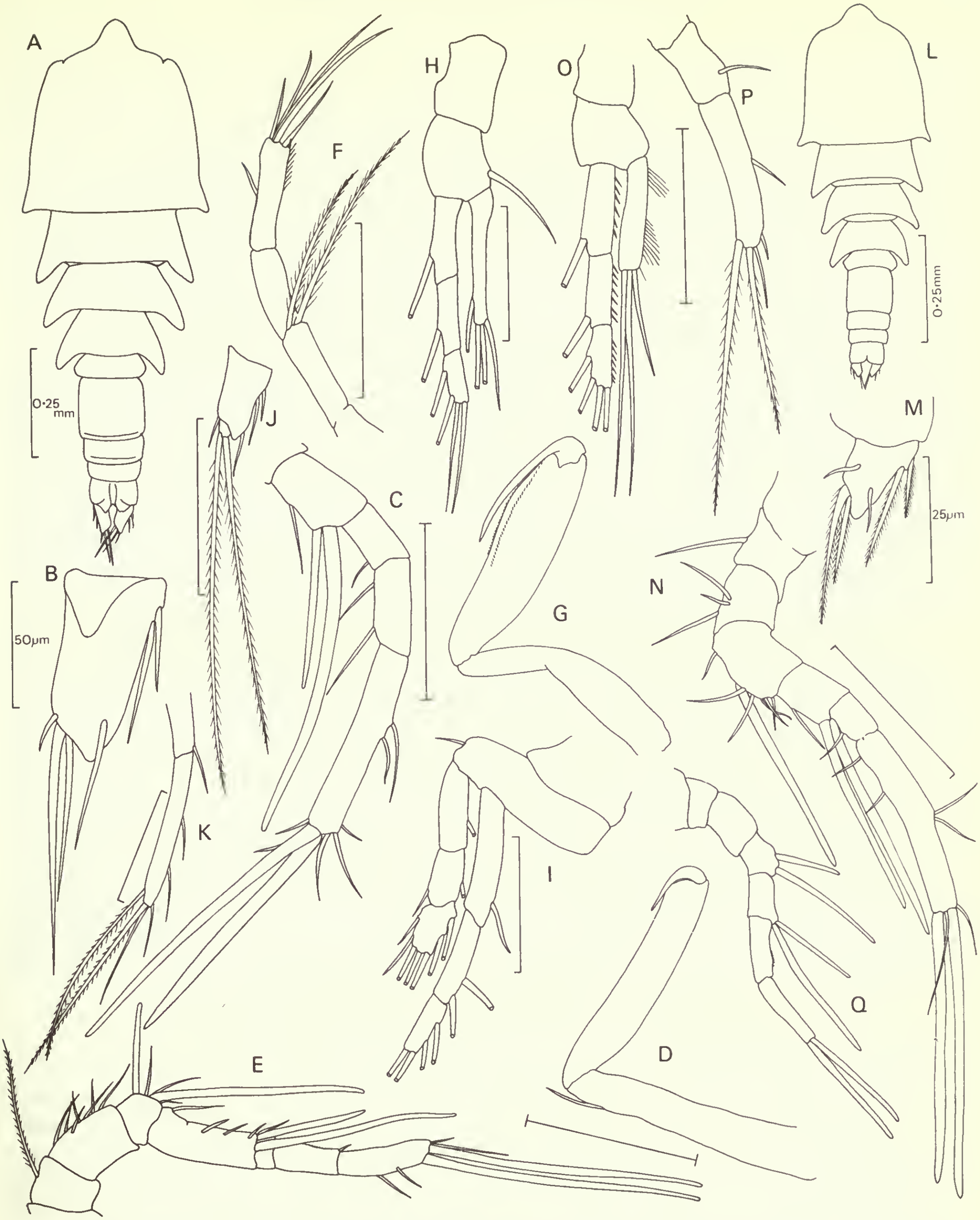

Fig. 15 *Clytemnestra scutellata*: A, female; B, caudal ramus; C, segments four to seven of first antenna; D, maxilliped; E, male first antenna; F, second antenna; G, maxilliped; H, first leg; I, second leg; J, caudal ramus; K, fifth leg. *C. rostrata*: L, female; M, caudal ramus; N, first antenna; O, first leg; P, fifth leg; Q, male first antenna. (Q redrawn from Giesbrecht, 1892.) Scales 0·1 mm unless otherwise indicated.

Clytemnestra rostrata (Brady, 1883)

Goniopsyllus rostratus Brady, 1883 : 107, pl. XLII, figs 9–16.

DIAGNOSIS. Caudal rami (Fig. 15M) about 1–1·1 times longer than wide. First antenna 7-segmented; ♀ with 1 aesthete on segment 4 and 2 each on segments 5 and 7, relative lengths of segments about 3 : 12 : 6 : 10 : 12 : 11 : 46 (Fig. 15N): ♂ with 2 aesthetes on segments 4, 5 and 7, relative lengths of segments about 4 : 7 : 16 : 8 : 14 : 23 : 28 (Fig. 15Q). Exopod of second antenna represented by 1 plumose seta. Basis of leg 1 (Fig. 15O) without outer margin seta; exopod with 3 distal setae. Leg 2 exopod segment 1 with an outer margin spine, exopod segment 3 with only 6 armature elements compared with 7 in *C. scutellata*: endopod segment 1 of legs 2–4 almost as long as exopod segments 1 and 2 combined. Free segment of leg 5 typically carrying 5 setae in both sexes (Fig. 15P), occasionally reduced to 4 setae.

Body length of ♀ from 0·60 to 1·00 mm, and ♂ from 0·80 to 0·90 mm.

MATERIAL EXAMINED. Holotype ♀ as *Goniopsyllus rostratus*: Challenger Expedition (Brady, 1883). BM(NH) registration number CC. 46. 1 ♀: Great Barrier Reef Expedition (Farran, 1936). BM(NH) registration number 1948.4.28.120. 7 ♀♀: Gulf of Guinea (Scott, 1894). BM(NH) registration numbers 1893.4.22.268–275.

REMARKS. The holotype of *C. rostrata* was described by Brady (1883) as a male, but re-examination of this specimen has shown it to be a female. It possesses a 7-segmented first antenna, with 1 aesthete on segment 4, and 2 aesthetes on segments 5 and 7. The relative lengths of segments 5, 6 and 7 are 12 : 9 : 36 respectively (as percentages of the total appendage length). The armature and proportional lengths of the segments indicate that this appendage belongs to a female.

Family **MIRACIIDAE**

DIAGNOSIS. Prosome 4-segmented with first thoracic somite fused to head, urosome 5-segmented in ♀ and 6-segmented in ♂. Body slender, slightly laterally compressed. Rostrum variable. Caudal rami longer than wide. First antenna 7- to 8-segmented in ♀, 8- to 9-segmented and haplocerate in ♂. Exopod of second antenna 1-segmented or absent. Mandible with small toothed blades and rudimentary palp. First maxilla with several cutting elements on arthrite, rest of appendage rudimentary. Second maxilla with small number of endites. Maxilliped well developed, 2-segmented with third segment apparently fused to short terminal claw. Leg 1 with 3-segmented exopod and 2-segmented endopod; legs 2–4 with 3-segmented rami except for leg 2 displaying sexual dimorphism with 2-segmented endopod in ♂. Leg 5 (♀) comprising a short baseoendopod bearing 3–5 setae and elongate exopod armed with 6 setae. Leg 5 (♂) with short baseoendopod bearing 2 or 3 setae, exopod bearing 4 or 6 setae.

Genus *MIRACIA* Dana, 1846

DIAGNOSIS. Cephalosome quite large, rounded anteriorly and provided with a pair of large cuticular lenses (Fig. 16A). Rostrum inconspicuous. Urosome somites 3–5 (6 in ♂) each provided with a row of spinules ventrally along posterior border. Caudal rami about 3 times longer than wide. Fitst antenna 8-segmented in ♀ carrying an aesthete on segment 4; in ♂ 9-segmented, with aesthete on segment 5 and geniculate between segments 6 and 7. Second antenna (Fig. 16B) with 1-segmented exopod bearing 2 apical plumose setae. Armature formula of legs 1–4 variable.

Leg 5 as in family diagnosis for both sexes. Leg 6 represented in ♂ by a small lateral lobe bearing 3 setae.

TYPE-SPECIES. *Miracia efferata* Dana, 1852.

REMARKS. The armature formula given by Lang (1948) for the genus *Miracia* applies only to *M. minor*, not *M. efferata*.

Miracia efferata Dana, 1852

Diagnosis. Cuticular lenses on cephalosome touching. Second antenna (Fig. 16B) with allobasis, as basis and first endopod segment completely fused. Armature formula of legs 1–4 as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1–I	0–1; 3	I–0; I–1; 4
Leg 2	0–0	1–0	0–1; 0–2; I, 1, 2	I–0; I–1; II, 2, 2
Leg 3	0–0	1–0	0–1; 0–2; I, 2, 2	I–0; I–1; III, 2, 3
Leg 4	0–0	1–0	0–1; 0–1; I, 2, 2	I–0; I–1; III, 2, 3

Legs 5 (♀) with 5 setae on baseoendopod and 6 setae on exopod (Fig. 16C). Leg 5 (♂) with 3 setae on baseoendopod and 6 setae on exopod (Fig. 16D).

Body length of ♀ from 1·45 to 2 mm and ♂ from 1·4 to 1·6 mm.

Material examined. 31 ♀♀, 8 ♂♂: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.196–205 (♀♀) and 1977.206–213 (♂♂).

Remarks. Both sexes of *M. efferata* were a bright bluish-purple colour even after a considerable time in preservative. The armature formula of legs 2–4 differs in several respects from that presented by Lang (1948) for the genus *Miracia*. The most significant differences are the presence of inner margin setae on endopod segment 1 of legs 2–4 and the presence of 3 outer margin spines on exopod segment 3 of legs 3 and 4. Lang's formula was presumably based only on data from *M. minor* Scott, 1894.

Miracia minor Scott, 1894

Diagnosis. Body (Fig. 16E) more slender than in *M. efferata* (c.f. Fig. 16A). Cuticular lenses on cephalosome not touching. Second antenna apparently with basis and 2-segmented endopod. Armature formula of legs 1–4 as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1–I	0–1; 3	I–0; I–1; 4
Leg 2	0–0	1–0	0–0; 0–2; I, 1, 2	I–0; I–1; II, 2, 2
Leg 3	0–0	1–0	0–0; 0–2; I, 2, 2	I–0; I–1; II, 2, 3
Leg 4	0–0	1–0	0–0; 0–1; I, 2, 2	I–0; I–1; II, 2, 3

Leg 5 (♀) with 4 setae on baseoendopod, 1 very long and plumose, and with 6 setae on exopod (Fig. 16G). Leg 5 (♂) with 2 setae on baseoendopod and 4 setae on exopod, 2 distally and 2 on the lateral margin (Fig. 16F).

Body length of ♀ from 0·90 to 0·93 mm and ♂ 0·82 to 0·93 mm.

Material examined. Syntype series ♀♀ and ♂♂: Gulf of Guinea (Scott, 1894). BM(NH) registration numbers 1893.4.22.340 and 1894.1.20.76–87. 1 ♀, 1 ♂: as *Macrosetella oculata*, John Murray Expedition (Sewell, 1947), BM(NH) registration numbers 1949.12.31.584–5. 1 ♀: Gulf of Aden. BM(NH) registration number 1911.11.8.43199.

Remarks. There is some confusion in the literature over the armature of the leg 5 in both sexes of *M. minor*. This arose because Scott (1894) in his original description illustrated 7 setae on the ♀ leg 5 exopod, and no outer margin seta on the baseoendopod. Examination shows that the armature of the ♀ leg 5 comprises 1 outer margin seta on the baseoendopod and 6 setae on the exopod in agreement with Giesbrecht (1895). Scott (1894) also figured the exopod of the ♂ leg 5 with 2 inner margin setae and 2 distal setae. The complete male specimen in the syntype series shows that in the slide (No. Z.D. 76) prepared by Scott the exopod had been accidentally rotated so the 2 outer margin setae (shown in Fig. 14F) appeared to be on the inner margin. Giesbrecht (1895) figured the ♂ leg 5 with 2 outer margin setae and 2 distal setae but most other authors (e.g. Owre and Foyo, 1967; Wells, 1970) redrew their illustrations from Scott (1894).

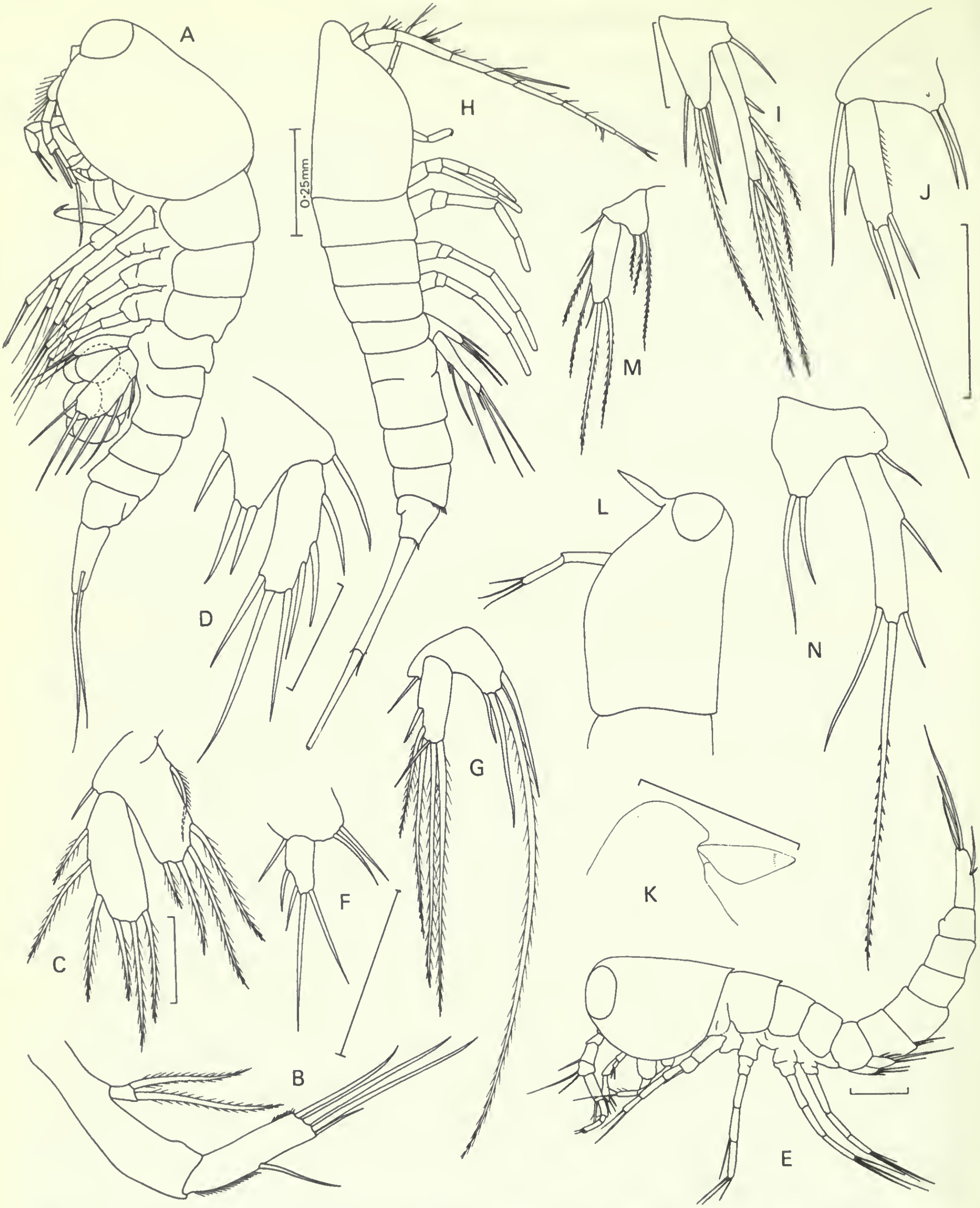

Fig. 16 *Miracia efferata*: A, female; B, second antenna; C, fifth leg; D, male fifth leg. *M. minor*: E, syntype male; F, fifth leg; G, female fifth leg. *Macrosetella gracilis*: H. female; I, fifth leg; J, male fifth leg; K, rostrum. *Oculosetella gracilis*: L, female cephalosome; M, fifth leg; N, male fifth leg. (L redrawn from Sars, 1916; M & N redrawn from Owre & Foyo, 1967.) Scales 0·1 mm unless otherwise indicated.

Genus *OCULOSETELLA* Dahl, 1895

DIAGNOSIS. As for type-species.

TYPE-SPECIES. *Oculosetella gracilis* (Dana, 1852).

Oculosetella gracilis (Dana, 1852)

Miracia gracilis Dana, 1852 : 46.
Setella oculata Sars, 1916 : 7, 13, Fig. VII.
Macrosetella oculata Rose, 1929 : 54.

DIAGNOSIS. Cephalosome rounded anteriorly, provided with large cuticular lenses touching in the median line. Rostrum large, clearly delimited at base and ventrally directed (Fig. 16L). Urosome somites 3–5 (6 in ♂) each provided with a spinule row ventrally along posterior border. Caudal rami about 3 times longer than wide. First antenna 7-segmented in ♀; 8-segmented and geniculate in ♂. Second antenna (Fig. 16L) with allobasis; exopod absent.

Leg 5 (♀) with 3 setae on baseoendopod and 6 setae on exopod (Fig. 16M). Leg 5 (♂) with 2 setae on baseoendopod and 4 setae on exopod (Fig. 16N).

Body length of ♀ from 1·2 to 1·35 mm and ♂ from 1·15 to 1·3 mm.

MATERIAL EXAMINED. None.

REMARKS. This species is rather incompletely known as some of its appendages have not been described. The two specimens of *Macrosetella oculata* reported by Sewell (1947) were found on re-examination to be *Miracia minor*.

Genus *MACROSETELLA* Scott, 1909

DIAGNOSIS. As for type-species.

TYPE-SPECIES. *Macrosetella gracilis* (Dana, 1848).

Macrosetella gracilis (Dana, 1848)

Setella gracilis Dana, 1848 : 155.

DIAGNOSIS. Cephalosome prolonged anteriorly (Fig. 16H), without cuticular lenses. Rostrum large, clearly delimited at base and ventrally directed (Fig. 16K). Caudal rami about 8 times longer than wide. First antenna 8-segmented in both sexes with aesthetes on segments 4 and 8. Second antenna with allobasis in ♀ and apparently with separate basis and 2-segmented endopod in ♂; exopod absent in both sexes. Mandible and first maxilla both comprising a toothed blade and a single seta representing the palp. Second maxilla with 1 (♂) and 2 (♀) endites. Maxilliped slender. Armature formula of legs 1–4 as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1–0	0–1; 3	I–0; I–0; 3
Leg 2	0–0	0–0	0–0; 0–2; I, 2, 1	I–0; I–1; II, 2, 2
Leg 3	0–0	0–0	0–1; 0–1; I, 2, 2	I–0; I–1; II, 2, 3
Leg 4	0–0	0–0	0–1; 0–1; I, 2, 2	I–0; I–1; II, 2, 3

Leg 5 (♀) with 4 setae on baseoendopod and 6 setae on exopod (Fig. 16I). Leg 5 (♂) with 2 setae on baseoendopod and 4 setae on exopod (Fig. 16J).

Body length of ♀ from 1·21 to 1·5 mm and ♂ from 1·13 to 1·16 mm.

MATERIAL EXAMINED. 21 ♀♀, 1 ♂: N.E. Atlantic Ocean, 18° N 25° W 'Discovery' Stn 7089. BM(NH) registration numbers 1977.214–223 (♀♀) and 1977.224 (♂).

REMARKS. This is the only member of the family Miraciidae without conspicuous cuticular lenses. It possesses only a simple eye spot.

SIPHONOSTOMATOIDA

This order as defined by Kabata (1979) comprises both the Caligoida, containing primarily parasites of fishes, and the Cyclopoida Siphonostoma, which are predominantly associated with or parasitic upon invertebrate hosts. Although adult and, more commonly, juvenile fish parasitic siphonostomatoids are occasionally recorded free in the plankton they are not true holoplanktonic forms and are not considered further. Siphonostomatoid copepods belonging to three genera, *Ratania* Giesbrecht, *Pontoeciella* Giesbrecht and *Hyalopontius* Sars (=*Megapontius* Hulsemann), have been found in the plankton of the N.E. Atlantic Ocean and can be regarded as members of the planktonic community. Species of these three genera are probably associated with planktonic invertebrates but no 'hosts' are known at present.

Family **RATANIIDAE**

Genus ***RATANIA*** Giesbrecht, 1891

DIAGNOSIS. Body unmodified; urosome 5-segmented in female, 6-segmented in male. Caudal ramus with 6-setae. Rostrum weakly developed. First antenna 5- to 7-segmented (♀) and 7- to 9-segmented (♂), with an aesthete on the terminal segment. Second antenna non-prehensile, 4-segmented and without trace of exopod. Oral cone short. Mandible an elongated blade, dentate apically and without palp. First maxilla bilobed; inner lobe with 3 equal setae, outer lobe with 3 setae and a short naked seta. Second maxilla 2-segmented, distal portion of second segment produced into a slightly curved claw. Maxilliped 3-segmented and with terminal claw armed with a spinulate seta.

Legs 1–4 with 3-segmented rami; armature formula for both sexes as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–1	1–0	0–1; 0–2; 1, 2, 3	I–1; I–1; II, 4
Leg 2	0–1	1–0	0–1; 0–2; 1, 2, 3	I–1; I–1; III, I, 4
Leg 3	0–1	1–0	0–1; 0–2; 1, I, 3	I–1; I–1; III, I, 4
Leg 4	0–1	1–0	0–1; 0–2; 1, I, 2	I–1; I–1; III, I, 4

Leg 5 with a free segment armed with 2 short medial and 3 long lateral setae.

Leg 6 represented by 2 small spines in the female and by a large postero-ventral flap bearing a single seta in the male.

TYPE-SPECIES. *Ratania flava* Giesbrecht, 1891.

REMARKS. *Ratania* shows a close affinity to the family Myzopontiidae, but differs from the genera of this family, primarily in the absence of an exopod on the second antenna, in the reduced number of segments in the first antenna, in the small oral cone and in the structure of the blade of the mandible (Heron & Damkaer, 1969).

Ratania flava Giesbrecht, 1891

DIAGNOSIS. *Female*. Prosome about 2·2 times longer than urosome. Ratio of lengths of urosome somites and caudal ramus (Fig. 17E) 14 : 30 : 12 : 11 : 16 : 17. Caudal ramus about 1·7 times longer than wide.

First antenna 5-segmented; relative lengths of segments (measured along posterior border) 23 : 7 : 5 : 35 : 30 (Fig. 17F); segmental armature elements I–6, II–2, III–2+1 aesthete, IV–5, V–5+2 aesthetes. Second antenna (Fig. 17G) with terminal seta about 3 times longer than distal segment. Tip of mandible (Fig. 17H) with two dentate areas well separated. Inner lobe of first maxilla (Fig. 17I) markedly longer than outer lobe. Free segment of leg 5 (Fig. 17E) somewhat expanded laterally, setae on leg 5 not conspicuously plumose.

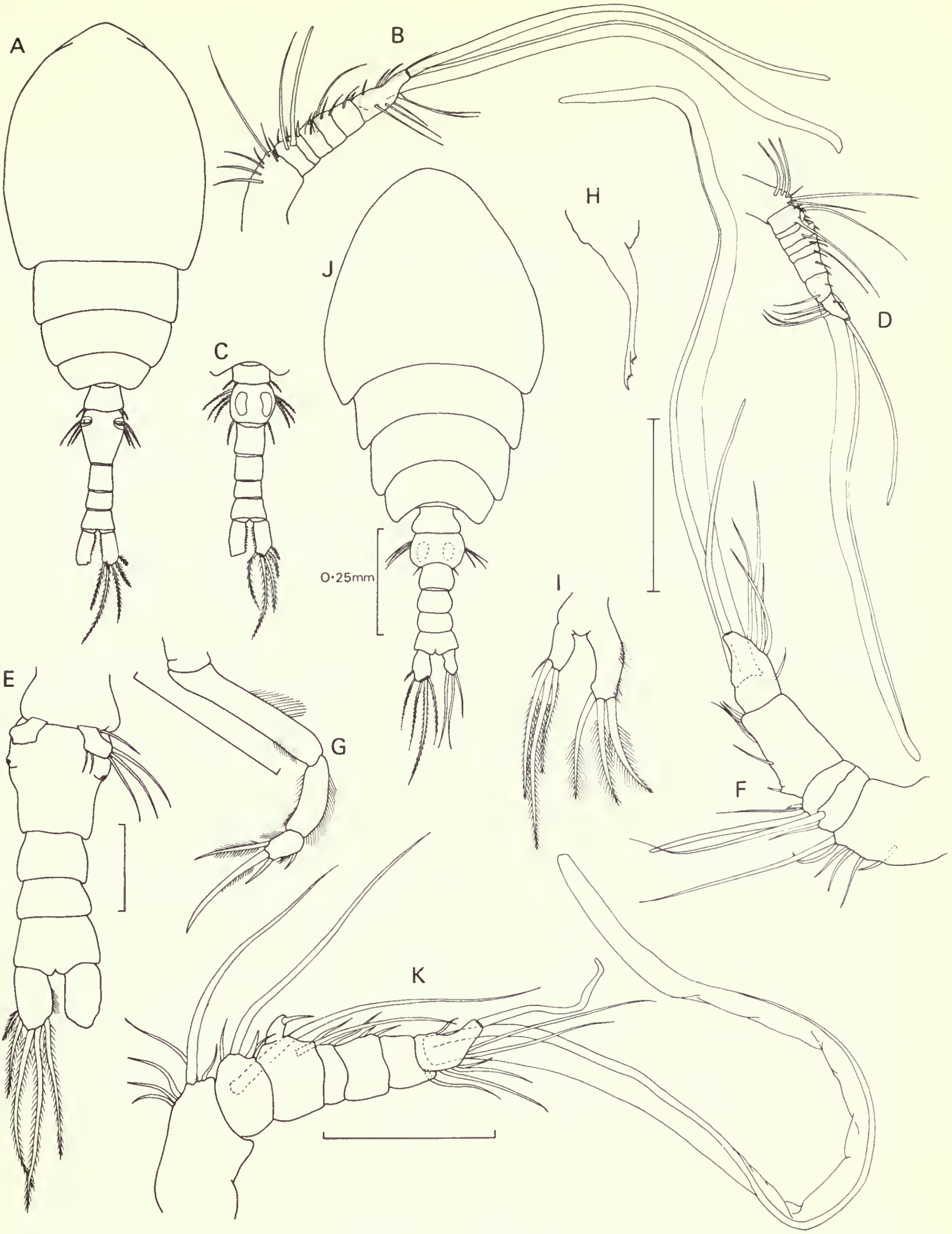

Fig. 17 *Ratania atlantica*: A, female; B, first antenna; C, male urosome; D, first antenna. *R. flava*: E, female urosome; F, first antenna; G, second antenna; H, mandible; I, first maxilla; J, male; K, first antenna. (A–D redrawn from Heron & Damkaer, 1969.) Scales 0·1 mm unless otherwise indicated.

Body length of female 1·1–1·2 mm.

Male. As for ♀ except: prosome about 1·9 times longer than urosome (Fig. 17J). Ratio of lengths of urosome somites and caudal ramus 14 : 16 : 14 : 13 : 11 : 14 : 18. First antenna (Fig. 17K) 7-segmented; relative lengths of segments 23 : 11 : 15 : 6 : 13 : 14 : 18. Segmental armature elements I–6, II–5, III–3, IV–1, V–2, VI–1, VII–6+2 aesthetes.

Body length of male 1–1·2 mm.

MATERIAL EXAMINED. 7 ♀♀ and 1 ♂; 'Discovery' Stn 7089. BM(NH) registration numbers 1977.242–248 (♀♀) and 1977.249 (♂).

REMARKS. Saraswathy (1961) reported that many of the segments of the 5-segmented first antenna in ♀ *R. flava* showed subdivisions. No significant subdivisions were observed in the present material, and the segmentation of the first antenna remains a useful character in distinguishing between the two species of *Ratania*.

Ratania atlantica Farran, 1926

DIAGNOSIS. *Female*. Prosome from 1·9 to 2·3 times longer than urosome (Fig. 17A); relative lengths of urosome somites and caudal ramus 14 : 29 : 15 : 10 : 13 : 19. Caudal ramus from 2·3 to 2·5 times longer than wide.

First antenna (Fig. 17B) 7-segmented, relative lengths of segments 25 : 8 : 4 : 8 : 9 : 13 : 33; segmental armature elements I–7, II–3+1 aesthete, III–2, IV–3, V–2, VI–2, VII–11+2 aesthetes. Tip of mandible with two dentate areas separated by small indentation. Inner lobe of first maxilla just longer than outer lobe. Free segment of leg 5 not markedly expanded laterally.

Body length 2·21–2·8 mm.

Male. Prosome about 1·9 times longer than urosome. Relative lengths of urosome somites and caudal ramus (Fig. 17C) 10 : 21 : 15 : 13 : 9 : 13 : 19. Caudal ramus about 2·2 times longer than wide.

First antenna (Fig. 17D) 9-segmented, relative lengths of segments 16 : 11 : 3 : 8 : 5 : 4 : 16 : 8 : 19; segmental armature elements I–4+3 aesthetes, II–4, III–2, IV–3; V–1, VI–1, VII–2, VIII–2+1 aesthete, IX–8+1 aesthete.

Body length 2·42–2·62 mm.

MATERIAL EXAMINED. Holotype ♀: Bay of Biscay (Farran, 1926). BM(NH) registration numbers 1926.12.6.40 (spirit) and 1926.12.6.52 (slide of appendages). 2 ♀♀: Antarctic (between 66° 30′ and 76° S), Terra Nova Stns 276 and 285 (Farran, 1929). BM(NH) registration numbers 1930.1.1.1330–1333 (spirit) and 1930.7.24.91 (slide of appendages).

REMARKS. The holotype of *R. atlantica* is in poor condition. The slide of the appendages contains one of the first antennae, it is 7-segmented and the relative lengths of the segments are as follows 24 : 11 : 4 : 11 : 10 : 11 : 29. The armature elements remaining on the appendage are in agreement with the formula given by Heron & Damkaer (1969). The body length of the holotype, 2·34 mm, also serves to distinguish between *R. atlantica* and the smaller *R. flava*. The two Antarctic specimens are poorly preserved, but their large size and the 7-segmented nature of the first antennae of one of them confirm that these specimens are *R. atlantica*.

Family **PONTOECIELLIDAE**

Genus ***PONTOECIELLA*** Giesbrecht, 1895

DIAGNOSIS. *Female*. Body unmodified (Fig. 18A), urosome 5-segmented. Caudal ramus with 6 setae, ventral seta strongly spinulate. Rostrum weakly developed. First antenna (Fig. 18C) 8-segmented with an aesthete on segment VI. Second antenna (Fig. 18D) non-prehensile, with a 1-segmented exopod bearing 1 or 2 apical setae. Oral cone long, forming a true siphon (Fig. 18B). Mandible (Fig. 18E) a slender, elongate blade without a palp. First maxilla (Fig. 18F) a single

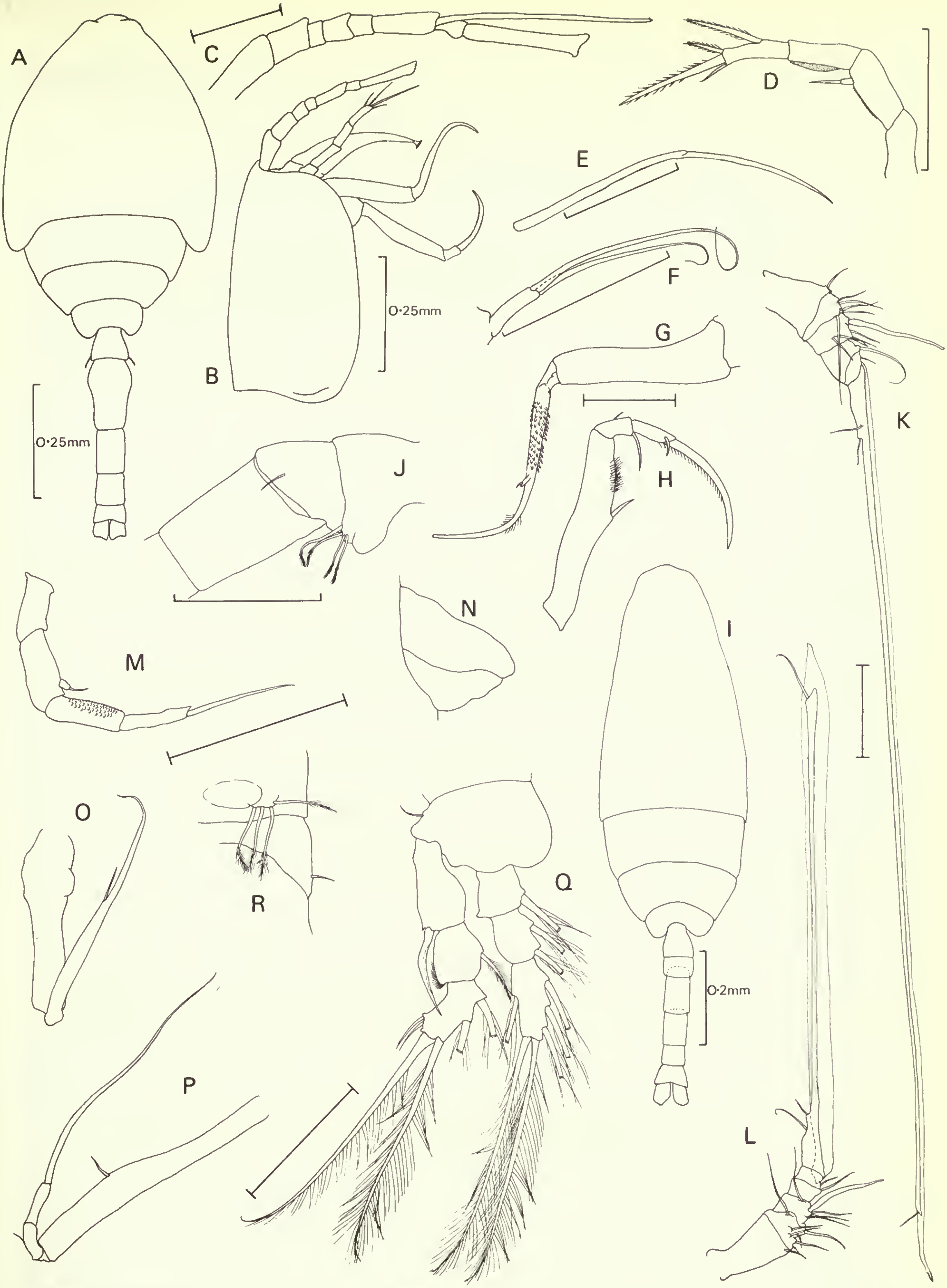

Fig. 18 *Pontoeciella abyssicola*: A, holotype female; B, female cephalosome lateral; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped; I, male; J, anterior portion of urosome, lateral; K, first antenna; L, first antenna from another specimen; M, second antenna; N, oral cone, lateral; O, second maxilla; P, maxilliped; Q, first leg; R, fifth and sixth legs. Scales 0·1 mm unless otherwise indicated.

lobe with 2 apical setae and (sometimes) a small spinule. Second maxilla (Fig. 18G) 2-segmented, distal segment curving through between 65 and 90°. Maxilliped (Fig. 18H) 4-segmented.

Legs 1–4 with 3-segmented rami; armature formula variable but usually as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–1	1–0	0–1; 0–2; 1, 2, 3	I–0; 0–1; I–II, I, 3
Leg 2	0–1	1–0	0–1; 0–2; 1, 2, 3	I–1; I–1; II, I, 3
Leg 3	0–1	1–0	0–1; 0–2; 1, I, 3	0–1; I–1; II, I, 3
Leg 4	0–1	1–0	0–1; 0–2; 1, I, 2	0–1; I–1; I, I, 3

Leg 5 reduced to a single seta.

Male. Body unmodified (Fig. 18I); urosome 6-segmented, first somite with ventral swelling (Fig. 18J), second somite narrower ventrally, producing slightly flexed appearance in lateral view. Ventral seta on caudal ramus thin-walled, not spinulate.

First antenna (Figs 18K, L) 6-segmented, the distal segment providing between 75 and 90% of the overall length of the appendage; one aesthete present on segment III and one on segment V, the latter adhering along the entire length of the distal segment and projecting beyond its tip. Second antenna (Fig. 18M) with 1-segmented exopod and 2-segmented endopod bearing a single apical element. Mouth cone (Fig. 18N) short without true siphon. Second maxilla (Fig. 18O), distal segment armed with a single naked seta. Maxilliped (Fig. 18P) 4-segmented, terminal claw long but weakly developed. Legs 1–4 (Fig. 18Q) as in female. Leg 5 (Fig. 18R) a small lobe fused to somite and bearing 4 plumose setae. Leg 6 represented by a single seta.

TYPE-SPECIES. *Pontoeciella abyssicola* (Scott, 1894).

REMARKS. The new species described by Ummerkutty (1968), *Danodes panikkari*, obviously belongs to *Pontoeciella*.

Pontoeciella abyssicola (Scott, 1894)

? *Artotrogus abyssicolus* T. Scott, 1894: 128–129, pl. 12, figs 5–9, pl. 14, figs 11–18.
Pontoeciella abyssicola Giesbrecht, 1895: 186.
Carnegiella gracilis Wilson, 1942: 176, figs 20–25.
Danodes plumata Wilson, 1942: 182–183, figs 57–68.
Danodes panikkari Ummerkutty, 1968; 298–304, figs 1–13.

DIAGNOSIS. As for genus (p. 240).

MATERIAL EXAMINED. Holotype ♀ (as *Artotrogus abyssicolus*): Gulf of Guinea 1° 55′ N 5° 55′ E (T. Scott, 1894). BM(NH) registration number 1893.4.22.69a. 4 ♀♀, 1 ♂: Great Barrier Reef Expedition, Stns 20, 28, 45 and 48 (Farran, 1936). BM(NH) registration numbers 1948.4.28.132–135. 92 ♀♀, 4 ♂: 'Discovery' Stn 7089, 18° N 25° W. BM(NH) registration numbers 1977.250–259 (♀♀) and 1977.260–263 (♂).

REMARKS. This species is highly variable both in the shape and proportions of the body and in the structure and armature of some of the appendages. Female body length varies from 0·7 mm (Farran, 1936) to 1·65 mm (Heron & Damkaer, 1969) and body width relative to length ranges from 33 to 41% (Farran, 1936). Variation in appendage structure and armature has been recorded from the first antenna to leg 5.

According to Ummerkutty (1968), in *Danodes panikkari* the seta representing the female leg 5 is absent. This difference alone is not sufficient to warrant the establishment of a distinct species, because of the variability exhibited by *P. abyssicola*, especially as this seta is often difficult to observe (T. Scott in his original description did not observe this seta although it is still present on his holotype specimen). *Danodes panikkari* is therefore regarded as a junior synonym of *Pontoeciella abyssicola*. The structure illustrated by Ummerkutty (1968, Fig. 7) as the first maxilla is not the first maxilla of a *Pontoeciella*, which is unilobed, and requires re-examination.

Less variation has been recorded in the males of *P. abyssicola*. However, a comparison of Farran's (1936, text-fig. 24d) and Wilson's (1942, fig. 20) figures with Fig. 16I shows variation in body form, especially in relative lengths of the urosome somites. The relative lengths of segments of the first antenna also vary markedly, with the distal segment providing between 75 and 90% of total appendage length. The male leg 5 is absent according to Scott (1894) and Wilson (1942), is represented by a single seta according to Farran (1936) or comprises four plumose setae (p. 242). Scott's male specimen is no longer extant but Farran's specimen from G.B.R. expedition Stn 20 was re-examined and the leg 5 was found to consist of 4 setae as in the 'Discovery' specimen illustrated in Fig. 18R. Only the most lateral seta is visible when the urosome is viewed from the dorsal aspect.

Family **MEGAPONTIIDAE**

Genus ***HYALOPONTIUS*** Sars, 1909

Syn. *Megapontius* Hulsemann, 1965.

DIAGNOSIS. Both sexes. Body unmodified. Urosome 5-segmented in female, 6-segmented in male. Caudal ramus with 2 lateral, 2 dorsal and 3 apical setae, the latter situated in a concave depression in the distal margin. Rostrum well developed, ventrally directed and sometimes truncate distally. First antenna 11-segmented; relative lengths of segments similar in all spp. 19 : 1 : 2 : 2 : 2 : 5 : 4 : 9 : 10 : 12 : 34; segmental armature usually as follows: I–6, II–1, III–2, IV–1; V–1, VI–6+1 spine, VII–1+1 spine, VIII–2, IX–2, X–2, XI–13+1 aesthete. Spine on segment VI usually pointed (Fig. 24E), that on segment VII often blunt (Figs 23D & 24E); aesthete on segment XI located near anterior margin about two thirds of distance along segment. Aesthete narrow and seta-like proximally, becoming thin-walled and flaccid distally. Second antenna 2- to 3-segmented; distal segment armed with a lateral spine, a small hirsute subapical seta and a very long terminal claw bearing a row of tiny spinules on its concave margin; exopod 1-segmented bearing lateral and medial naked setae and a sparsely pinnate apical seta.

Oral cone short and well developed, with elaborate buccal tube distally; buccal stylets present. Mandible an elongate blade, dentate at tip and without palp. First maxilla bilobed; larger inner lobe with 3 apical setae, outer lobe with small spine and a long spinulate seta apically. Second maxilla 2-segmented, distal segment curved and dentate towards apex. Maxilliped 3-segmented; first segment usually bearing a unilaterally pinnate seta; second segment with a naked seta and a row of hairs along inner margin; terminal segment bearing 2 subapical setae and a long apical claw armed with a row of tiny hairs.

Legs 1–4 with 3-segmented rami; armature formula within following range:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–1	1–0	0–1; 0–2; 1, 2, 3	(0–I)–1; (0–I)–1; (II–III), 2, 3
Leg 2	0–1	1–0	0–1; 0–2; 1, 2, 3	I–1; I–1; (II–III), I, 5
Leg 3	0–1	1–0	0–1; 0–2; 1, 2, 3	I–1; I–1; (II–III), I, 5
Leg 4	0–1	1–0	0–1; 0–2; 1, 2, 2	I–1; I–1; II, I, 5

Leg 5 comprising basal segment armed with an outer seta and free segment bearing 1 apical and 2 lateral setae. Leg 6 represented by a single seta in female and by a genital lobe bearing 1 long seta and 2 spinules in male.

TYPE-SPECIES. *Hyalopontius typicus* Sars, 1909.

REMARKS. Sars (1909) described *H. typicus* in detail and comparison of his description with that of *Megapontius gigas* (Hulsemann, 1965) clearly demonstrates that the two genera, *Hyalopontius* and *Megapontius*, are synonymous. Sars (1909) placed *Hyalopontius* in the monotypic Pontoeciellidae but there are significant differences between these two genera. Hulsemann (1965), with some reservations, referred *Megapontius* to the family Artotrogidae *sensu* Eiselt (1961). Heptner (1968) described a new species, *M. pleurospinosus*, and erected a new family the Megapontiidae for the genus. Although *Megapontius* is now recognized as a synonym of *Hyalopontius* the family name is unchanged as it was based on a generic name which was valid at the time it was proposed.

Key to species of HYALOPONTIUS (females only)

1 Outer margin spine present on exopod segment 1 of leg 1 3
– Outer margin spine absent from exopod segment 1 of leg 1 2
2 Exopod segment 3 of leg 2 with 2 outer margin spines . . . . . . ***H. alatus*** n. sp.
– Exopod segment 3 of leg 2 with 3 outer margin spines . . . . . ***H. hulsemannae*** n. sp.
3 Distal segment of second antenna with lateral seta situated about 33% of distance along margin; outer margin spine present on exopod segment 2 of leg 1 4
– This seta situated within proximal 25% of margin; outer margin spine absent from exopod segment 2 of leg 1 5
4 Exopod segment 3 of leg 1 with 2 outer margin spines . . . . ***H. typicus***
– Exopod segment 3 of leg 1 with 3 outer margin spines . . . . . ***H. pleurospinosus***
5 Distal seta on lateral margin of leg 5 free segment shorter than segment . . ***H. cinctus*** n. sp.
– This seta longer than segment 6
6 Exopod segment 3 of leg 2 with 2 outer margin spines; lateral setae on caudal rami situated in proximal one-third of ramus . . . . ***H. spinatus*** n. sp.
– Exopod segment 3 of leg 2 with 3 outer margin spines; lateral setae on caudal rami in distal one-third of ramus 7
7 Body length greater than 7 mm, body squat, about 2·9 times longer than greatest width; exopod of second antenna about 4·6 times longer than wide . . . . . ***H. enormis*** n. sp.
– Body length less than 6 mm, body about 4·3 times longer than greatest width; exopod of second antenna about 2 times longer than wide . . . . ***H. roei*** n. sp.

Hyalopontius typicus Sars, 1909

Megapontius gigas Hulsemann, 1965.

Diagnosis. *Female*. Body relatively squat, about 3·4 times longer than greatest width (Fig. 19A); prosome about 1·8 times longer than urosome. Rostrum rounded at apex. Epimeral plates of free thoracic somites 2 and 3 pointed but not markedly produced posteriorly. Relative lengths of urosome somites and caudal rami 18 : 27 : 12 : 6 : 14 : 23; first urosome somite without additional spinose processes near posterior border; dentate hyaline membrane absent from posterior border. Posterior border of genital complex with dentate hyaline membrane. Caudal ramus about 3–3·2 times longer than wide; lateral setae in distal half of ramus.

Relative lengths of first antenna segments 19 : 2 : 2 : 2 : 3 : 5 : 4 : 7 : 8 : 11 : 37 (Fig. 19C). Second antenna (Fig. 19D) exopod 1·9 times longer than wide; endopod 2-segmented with lateral spine on distal segment strongly developed and located about 35–38% of distance along segment; terminal claw longer than rest of appendage. Maxilliped segments 1 and 2 incompletely separated, distal segment with long terminal claw, a small naked subapical seta and a lateral seta, relative lengths of these 3 elements 61 : 7 : 32 respectively.

Legs 1–4 armature formula as for generic diagnosis except:

	Exopod
Leg 1	I–1; I–1; II, 2, 3
Leg 2	I–1; I–1; III, I, 5
Leg 3	I–1; I–1; II, I, 5

Leg 5 basal segment with small inner spinose process (Fig. 19E); free segment with 1 long apical and 2 medium-length lateral setae.

Body length of female 4·87–5·3 mm.

Male. Body similar to that of female; relative lengths of urosome somites and caudal ramus 16 : 13 : 15 : 12 : 7 : 15 : 22 (Fig. 19F). Appendages as in female (Figs 19H, I). Leg 6 (Fig. 19J) a small projection bearing a long outer plumose seta, and two inner, subequal spinules.

Body length of males 4·6–5·05 mm.

Material examined. 18 ♀♀. 7 ♂♂: N.E. Atlantic Ocean 44° N 12° W, 'Discovery' Stns 8508 78 (7 ♀♀) and 8509 20 (11 ♀♀, 7 ♂♂). BM(NH) registration numbers 1977.302–311 (♀) and 1977.312–318 (♂).

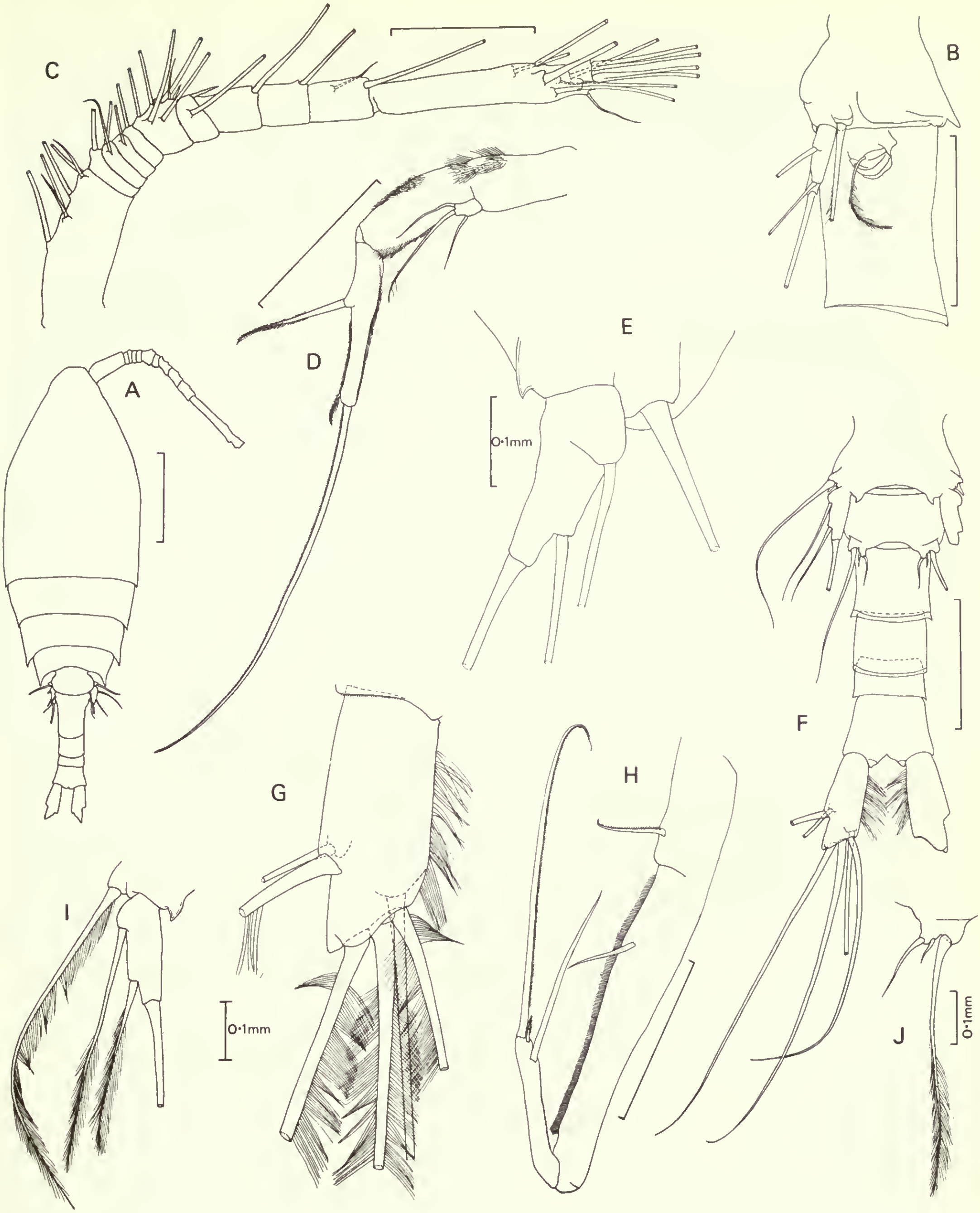

Fig. 19 *Hyalopontius typicus*: A, female; B, anterior portion of urosome; C, first antenna; D, second antenna; E, fifth leg; F, male urosome; G, caudal ramus; H, maxilliped; I, fifth leg; J, sixth leg. Scales 0·5 mm unless otherwise indicated.

REMARKS. The type material of *H. typicus* could not be located. It is not in the collections of the Musée Oceanographique de Monaco where the other material described in the same paper (Sars, 1909) is stored (Testa, pers. comm.). The present 'Discovery' material is identified as *H. typicus* because of the agreement in size and body proportions with the specimen figured by Sars (1909), and because of the position of the lateral spine on the distal segment of the second antenna. This spine was described by Sars as being in the middle of the segment but his figure shows it to be rather more proximal in position. The position of the lateral spine in the 'Discovery' material, at 35–38% of the distance along the margin of this segment, is sufficiently similar for these specimens to be regarded as conspecific with Sars' material. In contrast, the six new species of *Hyalopontius* described below have the lateral seta on the second antenna situated within the proximal quarter (25%) of the distal segment.

There are no significant differences between the material described above as *H. typicus* and *Megapontius gigas* Hulsemann, 1965, which is thus regarded as a synonym.

Hyalopontius hulsemannae sp. nov.

DIAGNOSIS. *Female.* Body slender (Fig. 20A), about 4 times longer than greatest width; prosome about 1·3 times longer than urosome. Rostrum rounded at tip (Fig. 20B). Epimeral plates of free thoracic somite 2 pointed but not markedly produced; those of free thoracic somite 3 produced posteriorly into a slender projection extending almost as far as the posterior border of the first urosome somite (Fig. 20C). Relative lengths of urosome somites and caudal ramus 14 : 31 : 15 : 8 : 20 : 12. Dentate hyaline membrane present along posterior margins of urosome somites 1–4. First urosome somite with 2 small spinose processes dorso-laterally near posterior border. Caudal ramus about 2·1 times longer than wide; lateral setae in distal half of ramus (Fig. 20D).

Relative lengths of first antenna segments; 19 : 2 : 2 : 2 : 2 : 5 : 4 : 9 : 10 : 10 : 35 (Fig. 20E). Second antenna (Fig. 20F) exopod about 2 times longer than wide; lateral spine on distal endopod segment small, unilaterally plumose and situated about 7% of the distance along segment. Mandible (Fig. 20G) with reduced number of dentate projections at tip. Maxilliped (Fig. 20H) segments 1 and 2 distinctly divided; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 77 : 7 : 16: respectively.

Legs 1–4 armature formula as for generic diagnosis except:

	Exopod
Leg 1	0–1; 0–1; II, 2, 3
Leg 2	I–1; I–1; III, I, 5
Leg 3	I–1; I–1; II, I, 5

Leg 5 (Fig. 20I) bearing a small blunt inner process on basal segment; free segment with long apical and 2 medium-length lateral setae.

Body length of holotype ♀ 5·03 mm.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean 20° N 21° W, 'Discovery' Stn 9541 22. BM(NH) registration number 1977.322.

REMARKS. The species is named after Kuni Hulsemann who provided the first well-illustrated account of a species in this genus. This species can be distinguished from other species, except *H. alatus* n. sp., by the absence of an outer margin spine from exopod segment 1 of leg 1. It differs from *H. alatus* primarily in the position of the lateral spine on the distal segment of the second antenna, the degree of expansion of the epimeral plates of free thoracic somites 2 and 3 and the possession of 3 outer margin spines on exopod segment 3 of leg 2 (as compared to 2 in *H. alatus*).

Hyalopontius alatus sp. nov.

DIAGNOSIS. *Female.* Body slender (Fig. 21A), about 5·2 times longer than greatest width; prosome about 1·3 times longer than urosome. Rostrum rounded at apex. Epimeral plates of free thoracic somite 2 produced, those of somite 3 markedly produced posteriorly and expanded laterally

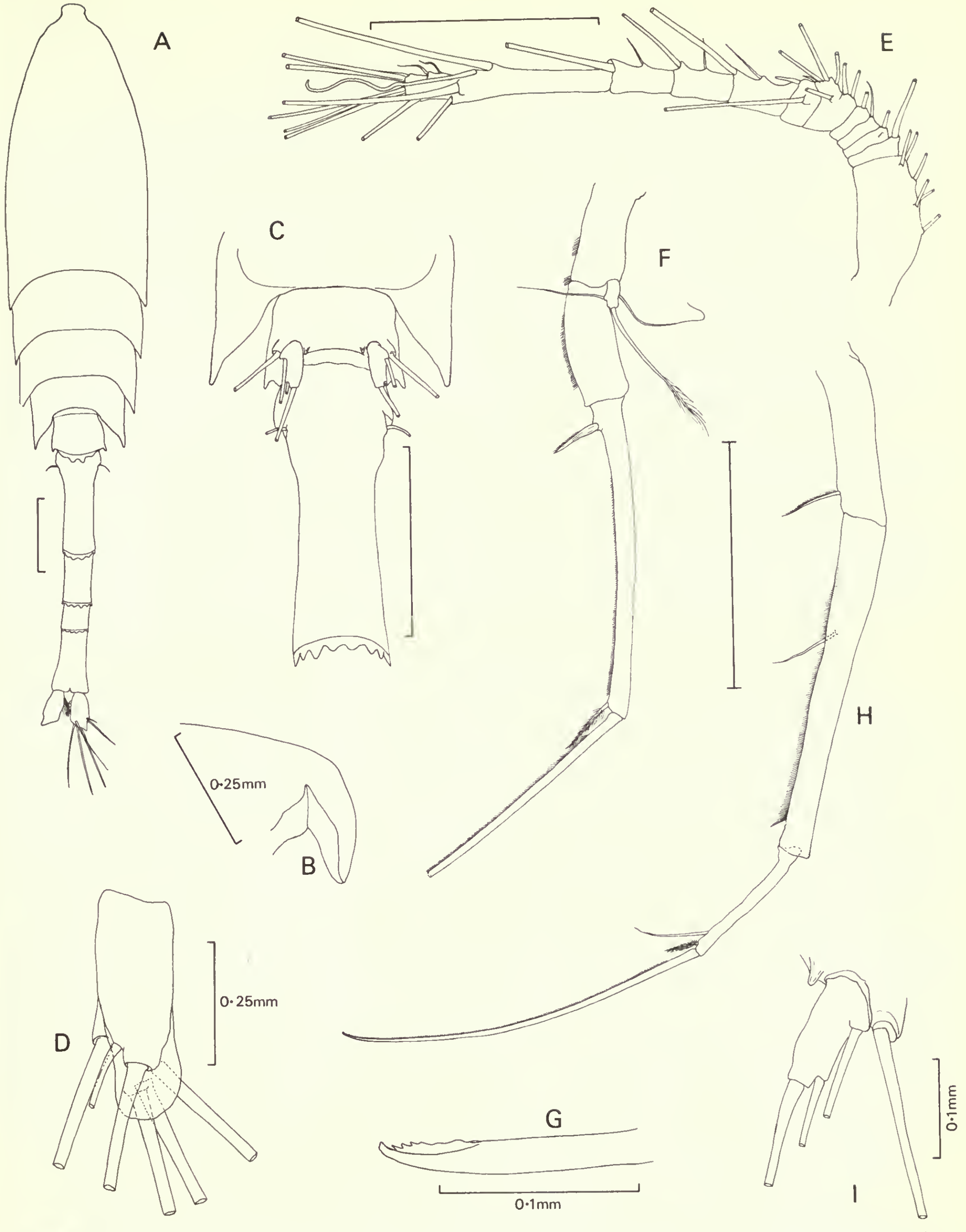
A
B
0·25mm
C
D
0·25mm
E
F
G
0·1mm
H
I
0·1mm

Fig. 20 *Hyalopontius hulsemannae* n. sp., holotype female: A, dorsal; B, rostrum; C, anterior portion of urosome; D, caudal ramus, lateral; E, first antenna; F, second antenna; G, tip of mandible; H, maxilliped; I, fifth leg. Scales 0·5 mm unless otherwise indicated.

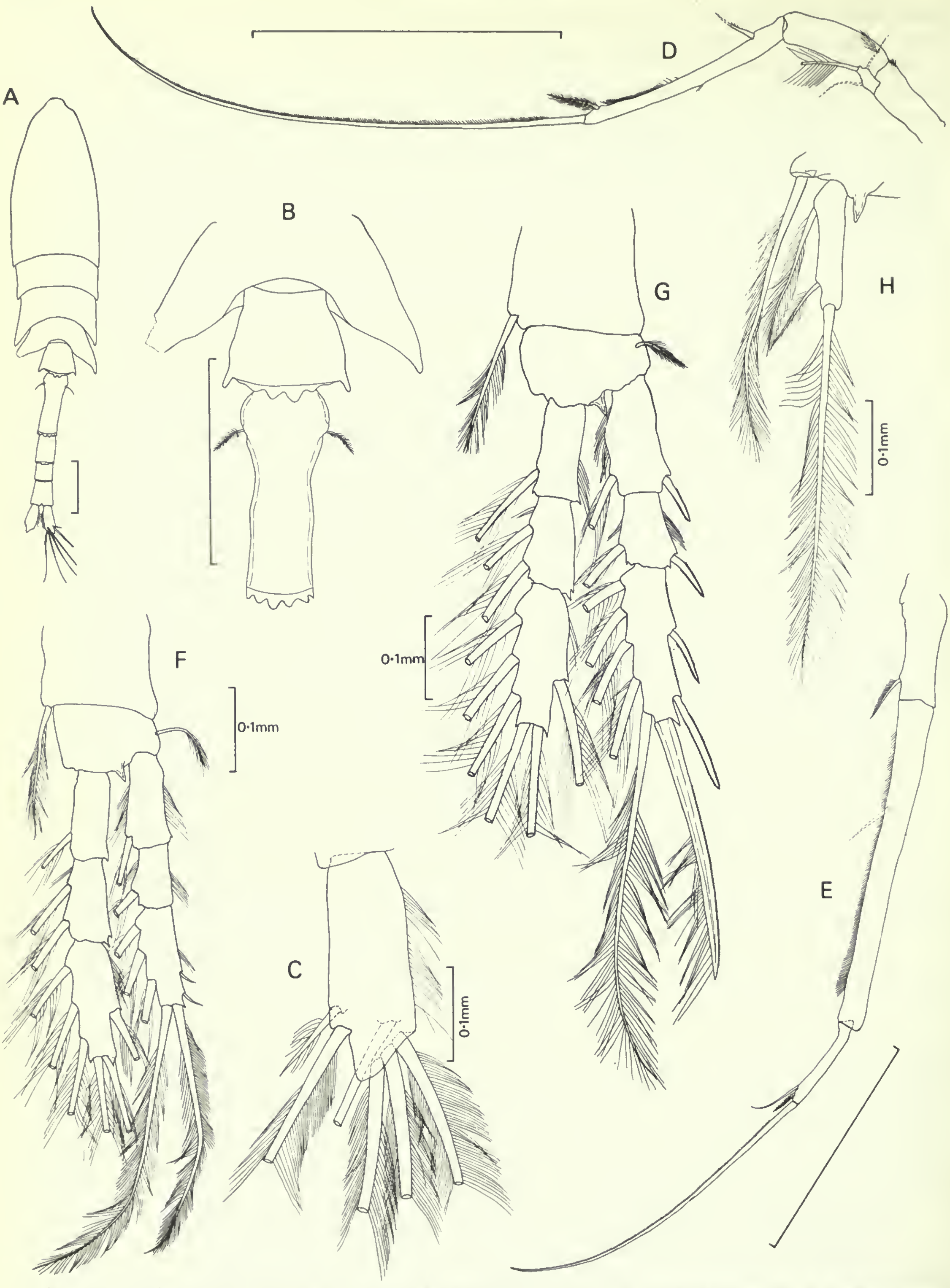
D
A
B
G
H
0·1mm
0·1mm
F
0·1mm
C
0·1mm
E
0·1mm

Fig. 21 *Hyalopontius alatus* n. sp., holotype female: A, dorsal; B, anterior portion of urosome; C, caudal ramus; D, second antenna; E, maxilliped; F, first leg; G, second leg; H, fifth leg. Scales 0·5 mm unless otherwise indicated.

(Fig. 21B). Relative lengths of urosome somites and caudal ramus 16 : 32 : 15 : 10 : 12 : 15. Dentate hyaline membrane present on posterior margins of urosome somites 1–4. First urosome somite with 2 small spinose processes dorso-laterally near posterior border. Caudal ramus (Fig. 21C) about 2·8 times longer than wide; lateral setae in distal half of ramus.

First antennae incomplete on both sides. Second antenna (Fig. 21D) exopod about 2 times longer than wide; lateral spine on distal endopod segment situated about 15% of distance along segment; terminal claw much longer than rest of appendage. Maxilliped (Fig. 21E) segments 1 and 2 distinctly divided; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 81 : 6 : 13 respectively.

Legs 1–4 (Figs 21F, G) armature formula as for generic diagnosis except:

	Exopod
Leg 1	0–1; 0–1; II, 2, 3
Leg 2	I–1; I–1; II, I, 5
Leg 3	I–1; I–1; II, I, 5

Leg 5 (Fig. 21H) with medium-sized spinose process on basal segment; distal seta on lateral margin of free segment shorter than the segment.

Body length of holotype ♀ 4·16 mm.

Material examined. Holotype ♀: N.E. Atlantic Ocean. 'Discovery' Stn 9541 24. BM(NH) registration number 1977.323.

Remarks. The specific name refers to the conspicuous wing-like expansion of the epimeral plates of free thoracic somite 3. This character, together with the armature formula of legs 1 and 2 and the position of the lateral spine on the distal segment of the second antenna, enables *H. alatus* to be distinguished from other species.

Hyalopontius spinatus sp. nov.

Diagnosis. *Female.* Body slender (Fig. 22A), about 5·1 times longer than greatest width; prosome about 1·2 times longer than urosome. Rostrum truncate at apex (Fig. 22D). Epimeral plates of free thoracic somites 1 and 2 markedly produced posteriorly, those of somite 3 pointed but not markedly produced. Relative lengths of urosome somites and caudal ramus 14 : 32 : 14 : 9 : 11 : 20. First urosome somite with a pair of dorso-lateral spinose processes near the posterior border (Figs 22B, C); dentate hyaline membrane present along posterior margins of urosome somites 1–4. Caudal ramus about 4·4 times longer than wide; lateral setae situated in proximal half of ramus.

Relative lengths of first antenna segments 17 : 1 : 1 : 2 : 2 : 5 : 3 : 10 : 12 : 13 : 34 (Fig. 22F); segmental armature as in generic diagnosis but with additional seta on segment II. Second antenna (Fig. 22F) exopod about 2·2 times longer than wide, lateral spine on distal segment small and situated about 10% of distance along segment; terminal claw much longer than rest of appendage. Mandible (Fig. 22G) with two areas of dentate projections. First maxilla (Fig. 22H) and second maxilla (Fig. 22I) as in other species of genus. Basal segment of maxilliped (Fig. 22J) with 2 strong processes on medial surface; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 83 : 8 : 9 respectively.

Legs 1–4 (Figs 22K, L) armature formula as for generic diagnosis except:

	Exopod
Leg 1	I*–1; 0–1; II, 2, 3
Leg 2	I–1; I–1; II, I, 5
Leg 3	I–1; I–1; II, I, 5

* This spine very small.

Leg 5 (Fig. 22M) with large blunt inner process on basal segment; free segment with long apical and 2 medium-length lateral setae.

Body length of holotype ♀ 4 mm.

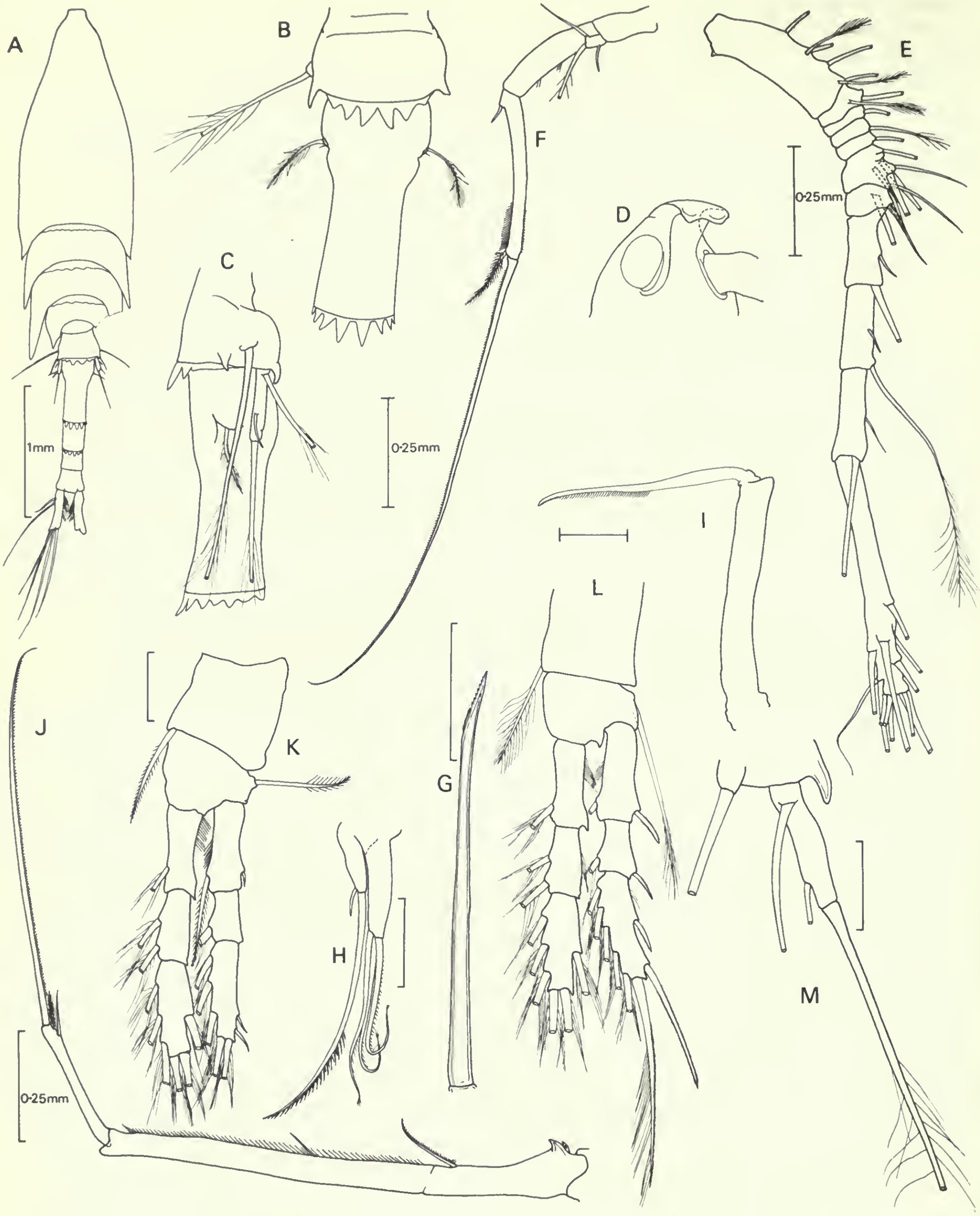
A
B
C
D
E
F
G
H
I
J
K
L
M
1mm
0·25mm
0·25mm
0·25mm

Fig. 22 *Hyalopontius spinatus* n. sp., holotype female: A, dorsal; B, anterior portion of urosome, dorsal; C, same, lateral; D, rostrum; E, first antenna; F, second antenna; G, mandible; H, first maxilla; I, second maxilla; J, maxilliped; K, first leg; L, second leg; M, fifth leg. Scales 0·1 mm unless otherwise indicated.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean 20° N 21° W, 'Discovery' Stn 9541 18. BM(NH) registration number 1977.271.

REMARKS. The specific name refers to the spinose processes formed by the development of the epimeral plates of free thoracic somites 1 and 2. This character, together with the armature formula of legs 1–4 and the position of the lateral setae of the caudal ramus in the proximal half of the ramus, serves to separate *H. spinatus* from other species.

Hyalopontius roei sp. nov.

DIAGNOSIS. *Female.* Body moderately elongate (Fig. 23A), about 4·3 times longer than greatest width; prosome about 1·3 times longer than urosome. Rostrum rounded at apex. Epimeral plates of free thoracic somites pointed but not markedly produced. Relative lengths of urosome somites and caudal ramus 15 : 32 : 15 : 9 : 14 : 15. Dentate hyaline membrane present on posterior margins of urosome somites 1–4. First urosome somite with 2 small dorso-lateral processes near posterior margin (Fig. 23B). Caudal ramus about 2·6 times longer than wide; lateral setae in distal half of ramus.

Relative lengths of first antenna segments 19 : 1 : 2 : 2 : 2 : 5 : 4 : 11 : 10 : 12 : 32 (Fig. 23C). Second antenna (Fig. 23E) exopod about 2 times longer than wide; distal segment of endopod with lateral spine situated about 21% of distance along segment; terminal claw longer than rest of appendage. Mandible (Fig. 23F) with complex tip comprising a row of dentate projections, a blade-like process and an apical portion. First maxilla (Fig. 23G) as in other species of genus. Basal segment of maxilliped (Fig. 23H) with 3 small bumps proximally on inner surface and not distinctly separated from segment 2; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 83 : 6 : 11 respectively.

Legs 1–4 (Fig. 23I) armature formula as for generic diagnosis except:

	Exopod
Leg 1	I–1; 0–1; II, 2, 3
Leg 2	I–1; I–1; III, I, 5
Leg 3	I–1; I–1; II, I, 5

Leg 5 (Fig. 23J) with large inner spinose process on basal segment; free segment with long apical seta and long proximal seta on lateral margin, distal seta just longer than segment.

Body length of holotype ♀ 5 mm.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean, 'Discovery' Stn 9131 23. BM(NH) registration number 1977.320.

REMARKS. This species is named after Dr Howard Roe who found most of the new *Hyalopontius* material described in this account. It can be distinguished by the combination of the following characters; the body proportions, the absence of marked epimeral plates, the position of the lateral spine at 21% of the distance along the distal segment of the second antenna endopod and the armature formula of legs 1–4.

Hyalopontius cinctus sp. nov.

DIAGNOSIS. *Female.* Body slender (Fig. 24A), about 4·7 times longer than greatest width; prosome about 1·3 times longer than urosome. Rostrum rounded at apex. Epimeral plates of free thoracic somite 2 slightly produced posteriorly; those of somite 3 also produced posteriorly but not reaching as far as posterior border of first urosome and not expanded laterally (Fig. 24B). Relative lengths of urosome somites and caudal ramus 14 : 37 : 14 : 9 : 14 : 12. Dentate hyaline membranes present around posterior borders of urosome somites 1–4. First urosome somite with a pair of large blunt processes situated dorso-laterally near posterior margin (Fig. 24B). Caudal ramus (Fig. 24C) about 2·4 times longer than wide; lateral setae in distal half of ramus.

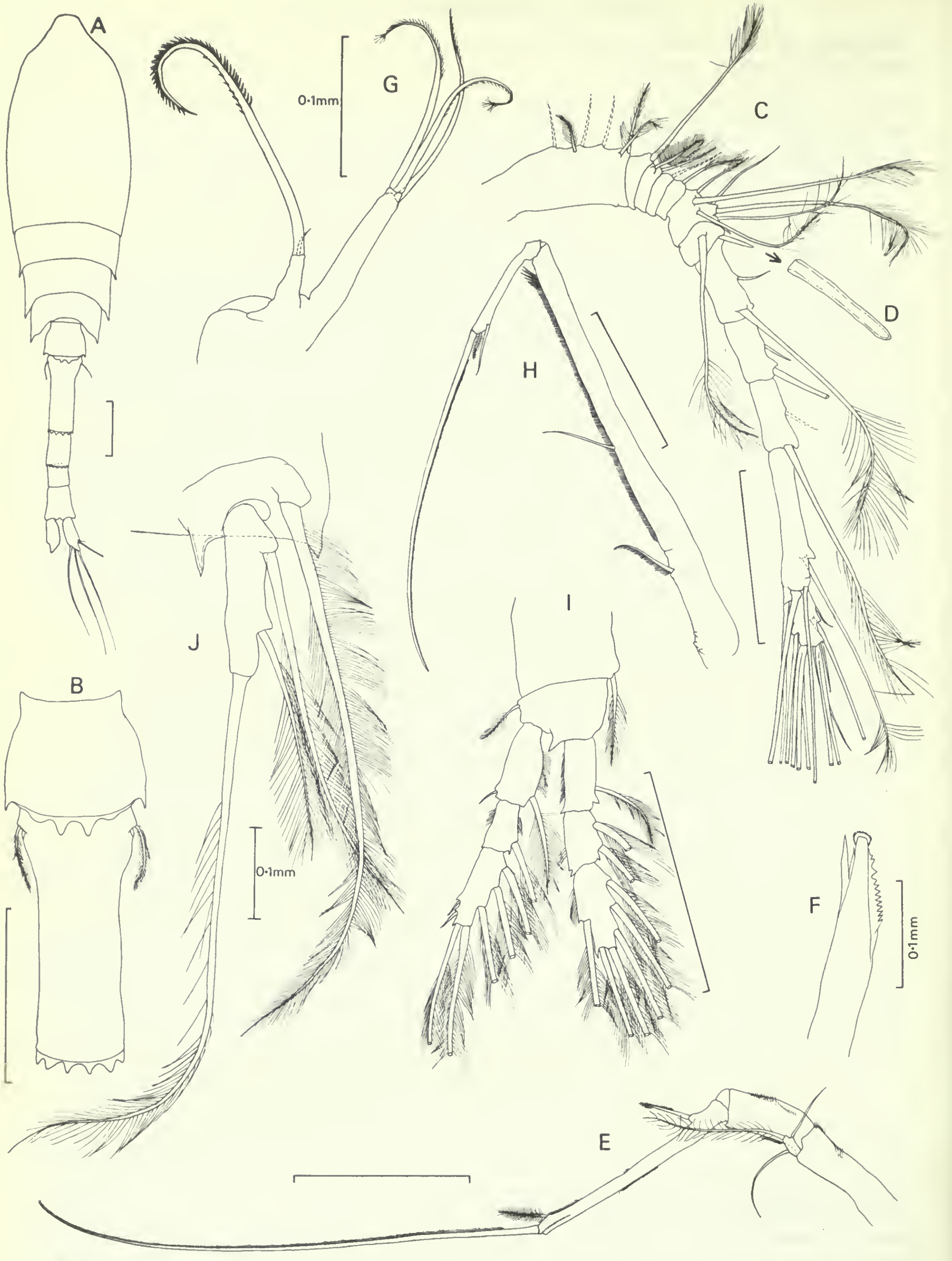

Fig. 23 *Hyalopontius roei* n. sp., holotype female: A, dorsal; B, anterior portion of urosome; C, first antenna; D, spine from first antenna seg. 7; E, second antenna; F, tip of mandible; G, first maxilla; H, maxilliped; I, first leg; J, fifth leg. Scales 0·5 mm unless otherwise indicated.

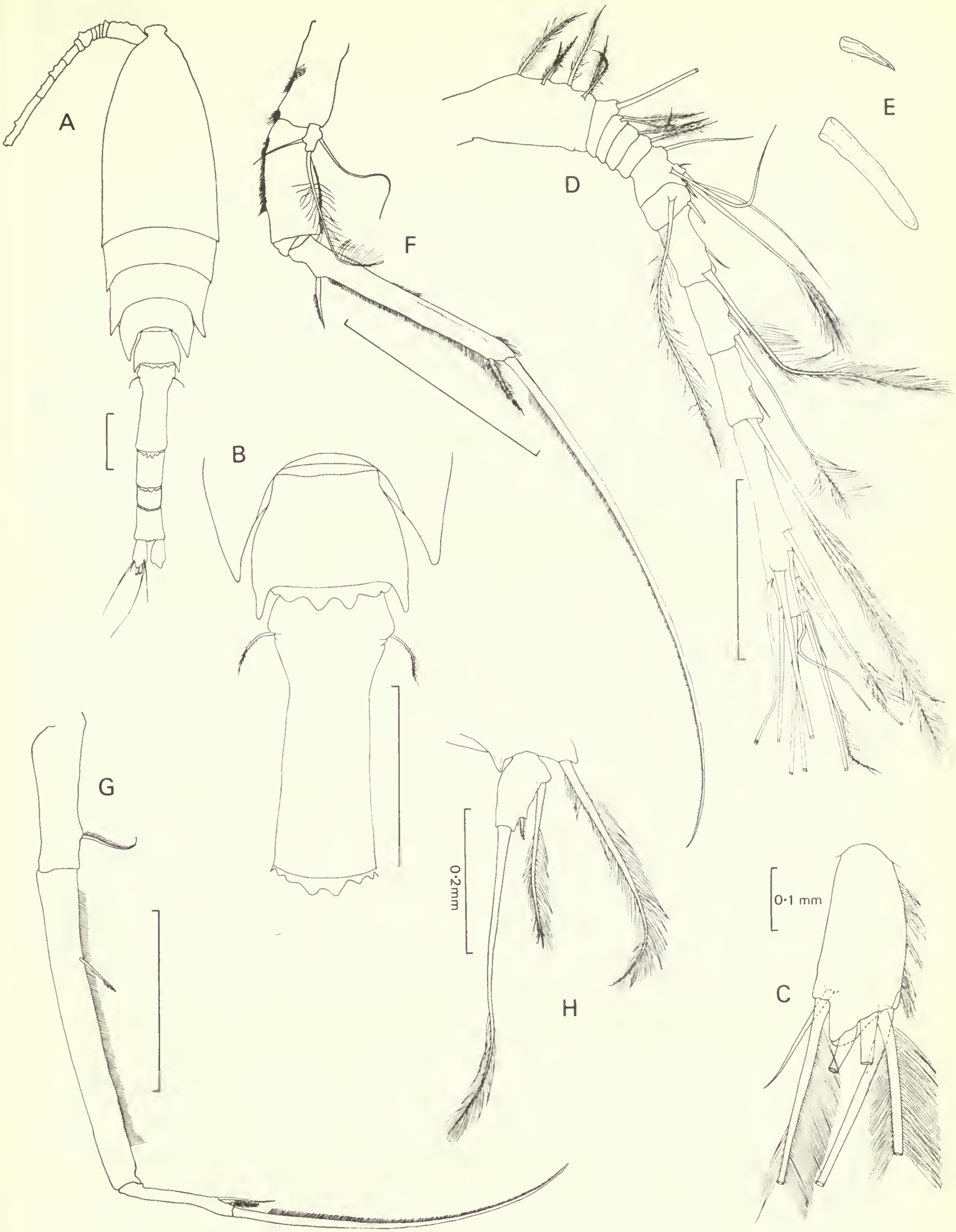

Fig. 24 *Hyalopontius cinctus* n. sp., holotype female: A, dorsal; B, anterior portion of urosome; C, caudal ramus; D, first antenna; E, spines from first antenna segs 6 & 7; F, second antenna; G, maxilliped; H, fifth leg. Scales 0·5 mm unless otherwise indicated.

Relative lengths of first antenna segments 20 : 1 : 2 : 2 : 2 : 5 : 4 : 10 : 11 : 11 : 32 (Fig. 24D). Second antenna (Fig. 24F) robust; exopod about 1·9 times longer than wide; distal segment of endopod with lateral spine positioned about 22% of distance along segment; terminal claw longer than rest of appendage. Segments 1 and 2 of maxilliped (Fig. 24G) distinctly separated; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 81 : 6 : 13 respectively.

Legs 1–4 armature formula as for generic diagnosis except:

	Exopod
Leg 1	I–1; 0–1; II, 2, 3
Leg 2	I–1; I–1; II–III*, I, 5
Leg 3	I–1; I–1; II, I, 5

* Two spines are present on one member and three on the other.

Leg 5 (Fig. 24H) with small inner process on basal segment; free segment with long apical seta, medium length proximal seta and very short distal seta on lateral margin.

Body length of holotype ♀ 4·94 mm.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean 20° N 21° W, 'Discovery' Stn 9131 23. BM(NH) registration number 1977.321.

REMARKS. The specific name of this species alludes to the distinctive leg 5. The short distal seta on the lateral margin of the free segment of leg 5 serves to distinguish *H. cinctus* from the other described species of the genus.

Hyalopontius enormis sp. nov.

DIAGNOSIS. *Female.* Body large, squat in appearance (Fig. 25A); about 2·9 times longer than greatest width; prosome about 2 times longer than urosome. Rostrum rounded at apex. Epimeral plates of free thoracic somites hardly produced at all. Relative lengths of urosome somites and caudal ramus 17 : 27 : 14 : 8 : 14 : 20. Smooth hyaline membranes present on posterior margins of urosome somites 1–4. First urosome somite without spinose processes. Genital complex very broad (Fig. 25B), only 1·1 times longer than greatest width. Caudal ramus (Fig. 25C) about 2·5 times longer than wide; lateral setae in distal half of ramus.

Relative lengths of first antenna segments 19 : 1 : 1 : 2 : 2 : 6 : 3 : 8 : 10 : 13 : 35 (Fig. 25D). Second antenna (Fig. 25E) robust, first endopod segment fused to basipod; exopod about 4·6 times longer than wide; lateral seta on distal segment of endopod positioned 20% of distance along segment; terminal claw shorter than rest of appendage. Mandible (Fig. 25F) with complex tip comprising dentate margin, trilobed apical portion and hirsute lateral portion. First maxilla (Fig. 25G) and second maxilla (Fig. 25H, I) as in other members of genus. Maxilliped (Fig. 25J) with segments 1 and 2 fused; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 74 : 5 : 21 respectively. Legs 1–4 (Figs 25K, L) as for generic diagnosis except:

	Exopod
Leg 1	I–1; 0–1; II, 2, 3
Leg 2	I–1; I–1; III, I, 5
Leg 3	I–1; I–1; II, I, 5

Leg 5 (Fig. 25M) with small inner process on basal segment; free segment with long apical seta and 2 lateral setae of medium length.

Body length of holotype ♀ 7·6 mm.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean 20° N 21° W, 'Discovery' Stn 9131 23. BM(NH) registration number 1977.319.

REMARKS. This is the largest known planktonic siphonostomatoid and can be distinguished from other species of the genus by its body proportions, the shape of the genital complex and the elongate exopod of the second antenna.

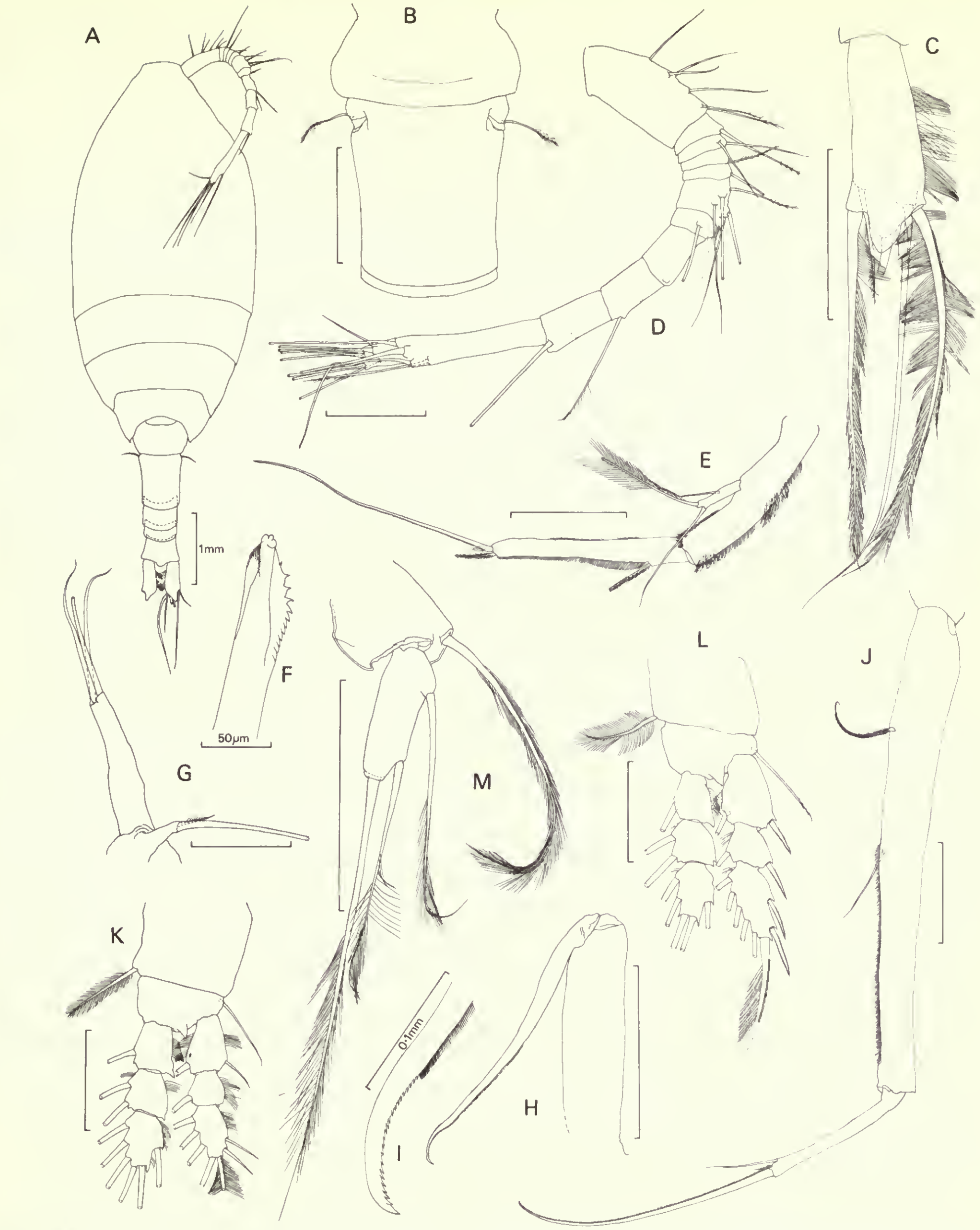

Fig. 25 *Hyalopontius enormis* n. sp., holotype female: A, dorsal; B, anterior portion of urosome; C, caudal ramus; D, first antenna; E, second antenna; F, tip of mandible; G, first maxilla; H, second maxilla; I, tip of second maxilla; J, maxilliped; K, first leg; L, second leg; M, fifth leg. Scales 0·5 mm unless otherwise indicated.

MORMONILLOIDA

The genus *Mormonilla* was first described by Giesbrecht in 1891, but because it exhibits a combination of podoplean and gymnoplean characters its position in the classification of the Copepoda is still uncertain. Giesbrecht (1891, 1892) placed it in a separate family, the Mormonillidae, within the Podoplea Ampharthandria, which also included the families Cyclopidae, Harpacticidae and Monstrillidae. The latter three families were raised to subordinal level by Sars (1901). Sars (1902) placed *Mormonilla* in the family Tortanidae of the Calanoida, but later (1913) changed this opinion, and stated that the systematic position of the genus is very doubtful though it may perhaps be regarded as the type of a very anomalous family of the gnathostomous Cyclopoida. Few authors have considered the systematic position of the Mormonillidae since Sars. Rose (1933) adopted a cautious approach and placed the Mormonillidae in the Podoplea, but did not assign this family to any of the existing suborders.

In a recent work which deals with copepod systematics (Kabata, 1979), a more natural arrangement of the podoplean line is attained with the recognition of six orders: Harpacticoida, Monstrilloida, Misophrioida, Siphonostomatoida, Poecilostomatoida and Cyclopoida. The Mormonillidae appear to be more closely related to the Misophrioida than to any other order, in possessing a podoplean arrangement of the body somites and typically gymnoplean mouthparts. However, *Mormonilla* differs from the two genera that comprise the aberrant Misophrioida (*Misophria* Boeck and *Benthomisophria* Sars) in the absence of a 'heart', the small number of segments in the first antenna and the complete absence of the fifth leg. *Mormonilla* resembles the cyclopoid genus *Oithona* Baird 1843 in general body facies and the structure of the first antenna, but the presence of a well-developed exopod on the second antenna suggests that the shared characters owe more to convergence than to a true phylogenetic relationship. It is therefore proposed to raise the family Mormonillidae to ordinal level.

Family **MORMONILLIDAE**

Genus *MORMONILLA* Giesbrecht, 1891

DIAGNOSIS. Body slender, cyclopiform (Fig. 26A); with 5-segmented prosome and 4-segmented urosome. Genital complex with paired ventral genital openings and spinose areas laterally. Caudal ramus longer than urosome, bearing 6 armature elements. First antenna 3- or 4-segmented. Second antenna (Fig. 26D) with 8-segmented exopod and 2-segmented endopod. Mandible (Fig. 26E) blade with strongly incised teeth; palp comprising large basis fused to endopod and 1-segmented exopod; both rami armed with 6 plumose setae. First maxilla (Fig. 26F) with well-developed basis; gnathobase small but distinct and bearing 8 armature elements; both exopod and endopod 1-segmented, armed with 6 and 8 setae respectively. Second maxilla (Fig. 26G) elongate, 5-segmented; proximal segment with 3 endites, second segment with 1 endite and an isolated seta; remaining 3 segments with 1, 1 and 4 armature elements. Maxilliped 2- or 3-segmented.

Legs 1–4 biramous; leg 1 with 2- or 3-segmented rami; leg 2 exopod 2- or 3-segmented, endopod 1- or 2-segmented; leg 3 with 1 segmented endopod and 2- and 3-segmented exopod; leg 4 with 1-segmented endopod and 2-segmented exopod.

Legs 5 and 6 absent.

Male unknown.

TYPE-SPECIES. *Mormonilla phasma* Giesbrecht, 1891.

Mormonilla phasma Giesbrecht, 1891

DIAGNOSIS. Widest part of genital complex in anterior third (Figs 26B, C). Lateral seta on caudal ramus situated about 33% of distance along ramus (Fig. 26A). First antenna 3-segmented, relative lengths of segments about 56 : 28 : 16. Maxilliped (Fig. 26H) 2-segmented; proximal segment with 6 medial margin setae, distal segment with 7 setae.

Leg 1 (Fig. 26I) with spinose inner projections on coxa, basis and endopod segments; both rami 2-segmented; legs 2–4 with 2-segmented exopods and 1-segmented endopods; armature formula as follows.

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	0–0	0–0; 0, 2, 2	I–0; III, 2, 3
Leg 2	0–0	0–0	0, 2, 1	0–0; I, 1, 5
Leg 3	0–0	0–0	0, 2, 1	0–0; 0, 1, 4
Leg 4	0–0	0–0	0, 2, 1	0–1; 0, 1, 3

Body length of female from 1·58 to 1·73 mm.

MATERIAL EXAMINED. 1507 ♀♀: N.E. Atlantic, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.272–281.

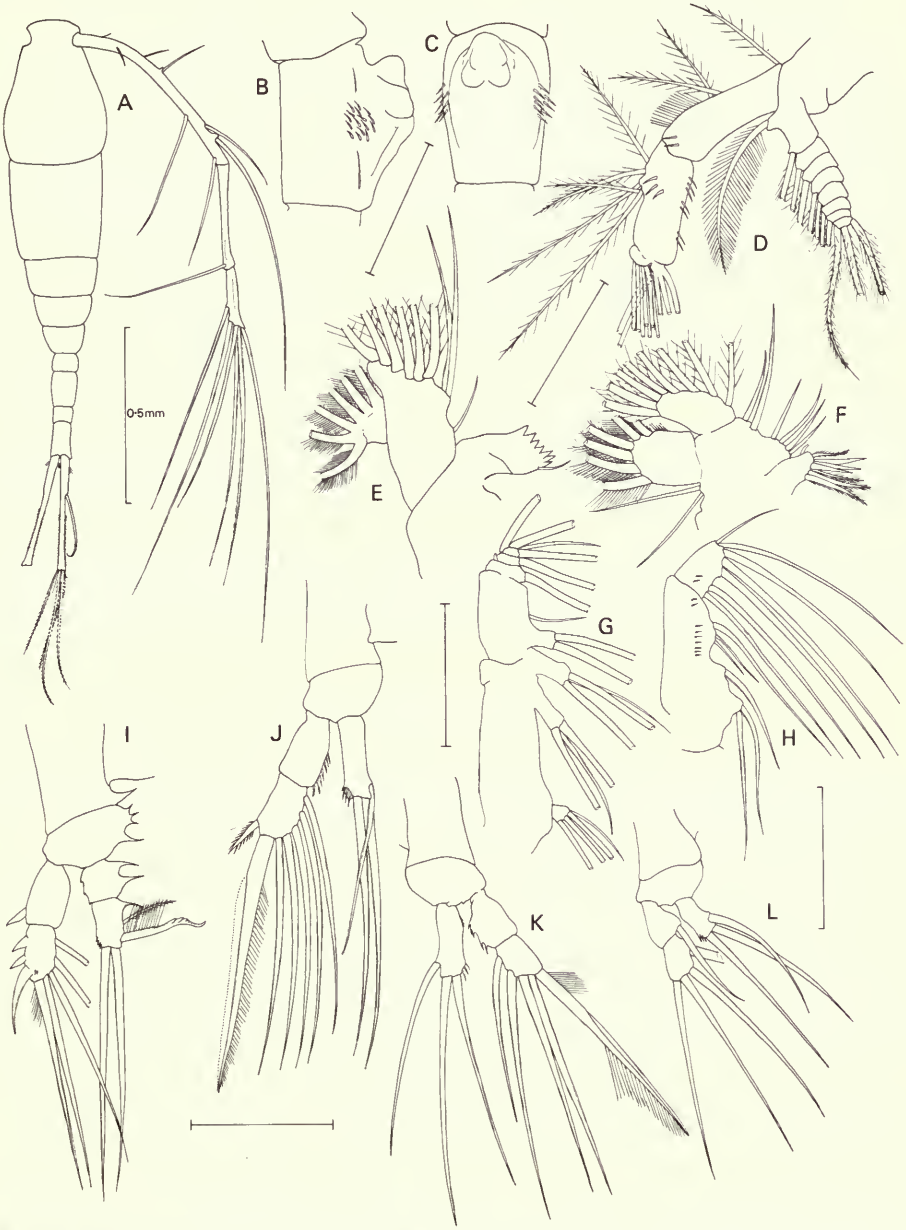

Fig. 26 *Mormonilla phasma*: A, female; B, genital complex, lateral; C, same, ventral; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped; I, first leg; J, second leg; K, third leg; L, fourth leg. Scales 0·1 mm unless otherwise indicated.

Remarks. This species is most readily distinguished by the position of the lateral seta on the caudal ramus when sorting through large samples of *Mormonilla*. Other significant differences are found in the segmentation of the first antennae and legs 1–3.

Mormonilla minor Giesbrecht, 1891

Mormonilla minor Giesbrecht, 1891 : 474.
Mormonilla polaris Sars, 1900 : 120–126, pl. XXXIV.
Mormonilla atlantica Wolfenden, 1905 : 16.

Diagnosis. Widest part of genital complex about at mid-point (Fig. 27B). Lateral seta on caudal ramus located about 16% of distance along ramus (Fig. 27A). First antenna 4-segmented, relative lengths of segments about 25 : 28 : 25 : 22 (Fig. 27C). Maxilliped (Fig. 27D) indistinctly 3-segmented; proximal segment with 7 setae on medial margin, middle segment with 1 seta and distal segment with 5 setae. Leg 1 (Fig. 27E) with fringes of strong setules on inner margins of coxa, basis and endopod; both rami usually 3-segmented; leg 2 (Fig. 27F) with 3-segmented exopod and 2-segmented endopod; leg 3 with 3-segmented exopod and 1 segmented endopod; leg 4 with 2-segmented exopod and 1-segmented endopod. Armature formula as follows:

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	0–0	0–0; 0–0; 0, 2, 1	I–0; I–1; II, 1, 3
Leg 2	0–0	0–0	0–0; 0, 2, 1	0–0; 0–1; I, 1, 4
Leg 3	0–0	0–0	0, 2, 1	0–0; 0–1; 0, 1, 3
Leg 4	0–0	0–0	0, 2, 1	0–1; 0, 1, 3

Body length of female from 1·2 to 1·38 mm.

Material examined. 274 ♀♀: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.282–291.

Remarks. The segmentation of the first pair of swimming legs is rather variable with the leg 1 endopod being either 2- (Giesbrecht, 1891, 1892) or 3-segmented (Sars, 1900; Wolfenden, 1905). This variation appears to reflect merely the degree of separation of the two distal segments and is not regarded as significant (Farran, 1908).

Species depth distributions

The depth distribution data for all of the species recorded from the 'Discovery' Station 7089 Day and Night series are given in Table 3. The vertical migration patterns of the more abundant species are discussed below.

Aegisthus mucronatus: During the day female *A. mucronatus* were found between 210 and 790 m and over 80% of the population was concentrated at 210–290 m. At night the depth range was greater, 25–785 m, and there was some evidence of both upward and downward night scattering as 89% of the population was distributed between 110 and 400 m. The data for the males (Table 3) also provide some evidence of an upward vertical migration at night.

Aegisthus aculeatus: This species was distributed quite uniformly between 700 and 1220 m in the daytime. During the night the depth range was virtually the same although a small number of specimens was recorded at 505–700 m. The population appeared to be more concentrated at night as 86% of individuals were found between 800 and 1010 m. *A. aculeatus* was the dominant harpacticoid between 700 and 1250 m whilst its congener, *A. mucronatus*, was dominant in the 110–500 m depth range. There was little vertical overlap between the distribution of these two species.

Miracia efferata: *M. efferata* was found only within the upper 100 m of the water column both day and night and there is little evidence of any diurnal change in depth distribution.

Other harpacticoid species: The remaining species occurred in small numbers within the following depth ranges: *Macrosetella gracilis*, 55–300 m; *Clytemnestra scutellata*, 10–60 m; *Microsetella*

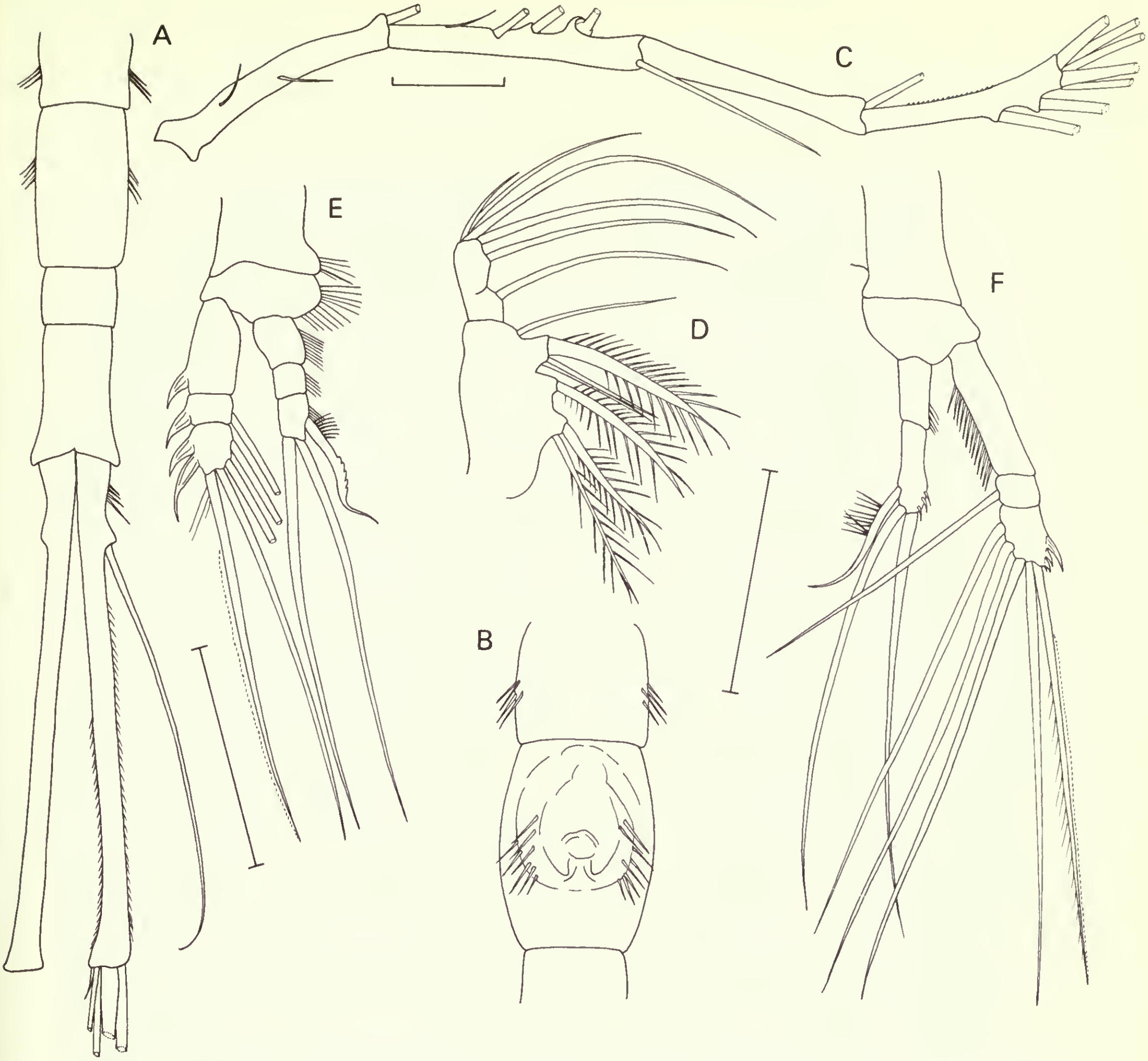

Fig. 27 *Mormonilla minor*: A, female urosome; B, genital complex, ventral; C, first antenna; D, maxilliped; E, first leg; F, second leg. Scales 0·1 mm.

norvegica, 0–290 m; *Neotisbella gigas*, 300–900 m; *Volkmannia forficula*, 410–900 m; *Bathyidia remota* 1000–1250 m and *Volkmannia attenuata* 3760–3920 m.

Pontoeciella abyssicola: Females were recorded between 112 and 600 m during the day, with about 57% of the population distributed above 400 m. At night the depth range was 110–700 m and over 76% of the population was concentrated above 400 m. This indicates that an upward vertical migration of at least part of the population had occurred.

Other siphonostomatoid species: Small numbers of *Ratania flava* were found between 20 and 200 m. The species of *Hyalopontius* were recorded from the following depths: *H. typicus*, 2500–3100 m and 3000–3500 m; *H. hulsemannae*, 3740–3870 m; *H. alatus*, 3000–3500 m; *H. spinatus*, 3830–4060 m; *H. roei*, 3000–3500 m; *H. cinctus*, 3000–3500 m and *H. enormis* 3000–3500 m.

Mormonilla phasma: This species occurred primarily between 410 and 1250 m, with only occasional specimens taken in shallower hauls. The day and night depth distributions were similar with between 70 and 75% of the population concentrated at 410–700 m in the shallow mesopelagic zone.

Table 3 Species composition of the day and night series taken at 'Discovery' Station 7089 (18° N 25° W). (The numbers given are the estimated totals. contaminates are given in parentheses)

Day series	*Aegisthus mucronatus*		*Aegisthus aculeatus*		*Micro-setella norvegica*	*Volk-mannia forficula*		*Neotis-bella gigas*	*Clytem-nestra scutellata*	*Miracia efferata*		*Macro-setella gracilis*		*Pontoe-ciella abyssicola*		*Ratania flava*	*Mor-monilla phasma*	*Mor-monilla minor*
Depth (m)	♀	♂	♀	♂	♀	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♀	♀
10–0	–	–	–	–	8	–	–	–	–	40	–	–	–	–	–	–	–	–
20–10	–	–	–	–	–	–	–	–	32	256	96	–	–	–	–	–	–	–
50–20	–	–	–	–	–	–	–	–	–	128	–	–	–	–	–	–	–	–
100–55	–	–	–	–	–	–	–	–	–	32	–	64	32	–	–	64	–	–
194–112	–	–	–	–	–	–	–	–	–	–	–	48	–	64	–	16	–	–
290–210	2240	160	–	–	16	–	–	–	–	–	–	96	–	128	16	–	–	16
400–305	272	32	–	–	–	–	–	–	–	(24)	(8)	–	–	64	24	–	24	–
500–410	224	8	–	–	–	8	–	–	–	(8)	–	–	–	144	–	–	1272	384
600–515	8	–	–	–	–	24	–	–	–	–	–	–	–	48	–	–	1456	152
700–610	16	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	240	88
790–700	8	–	104	–	–	–	–	–	–	–	–	(8)	–	–	–	–	88	8
890–800	–	–	112	–	–	8	–	8	–	–	–	–	–	–	–	–	136	–
1020–910	–	–	184	16	–	–	–	–	–	–	–	–	–	(8)	–	–	544	–
1220–1000	–	–	112	–	–	–	–	–	–	–	–	–	–	–	–	–	220	8
Totals =	2768	200	512	16	24	40	8	8	32	456	96	208	32	448	40	80	3980	656

Table 3 Continued

Night series Depth (m)	*Aegisthus mucronatus*		*Aegisthus aculeatus*		*Bathyidia remota*	*Volkmannia forficula*		*Neotisbella gigas*		*Clytemnestra scutellata*	*Miracia efferata*		*Macrosetella gracilis*	*Pontoeciella abyssicola*	*Ratania flava*		*Mormonilla phasma*	*Mormonilla minor*
	♀	♂	♀	♂	♂	♀	♂	♀	♂	♀	♀	♂	♀	♀	♀	♂	♀	♀
10–0	–	–	–	–	–	–	–	–	–	–	64	–	–	–	–	–	–	–
25–10	–	–	–	–	–	–	–	–	–	–	–	64	–	–	–	–	–	–
60–25	32	–	–	–	–	–	–	–	–	32	160	96	–	–	32	–	–	–
100–49	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
200–110	544	400	–	–	–	–	–	–	–	–	–	–	48	144	32	16	–	–
300–210	352	32	–	–	–	–	–	–	–	–	–	–	80	112	–	–	–	–
400–300	560	40	–	–	–	–	–	8	–	–	–	–	–	128	–	–	–	–
500–410	96	–	–	–	–	16	–	–	–	–	–	–	–	56	–	–	1840	448
600–505	32	8	8	–	–	8	–	–	–	–	–	–	(8)	56	–	–	2112	480
700–610	8	–	–	16	–	–	8	–	8	–	–	–	–	8	–	–	1688	384
785–700	8	–	16	–	–	–	–	16	–	–	–	–	–	–	(8)	–	920	168
900–800	–	–	296	–	–	–	–	16	–	–	–	–	–	–	–	–	640	32
1010–900	(8)	–	184	24	–	–	–	–	–	–	–	–	–	–	–	–	456	8
1250–1000	–	–	52	–	4	–	–	–	–	–	(12)	–	–	–	–	–	100	8
Totals =	1632	480	556	40	4	24	8	40	8	32	224	160	128	504	64	16	7756	1528

Mormonilla minor: *M. minor* has an almost identical depth distribution to that of *M. phasma*. The depth range is basically 410–1220 m with isolated records from shallower hauls. The distribution is slightly more concentrated in the 410–700 m depth zone with between 86 and 95% of the population occurring there.

The similarity between the depth distributions of the two species of *Mormonilla* is remarkable because the other two pairs of closely related forms found in the mesopelagic zone (i.e. the two species of *Aegisthus* and the two forms of *Oncaea ornata* Giesbrecht) both exhibit a marked degree of vertical segregation (see Boxshall, 1977*a* for *Oncaea ornata*).

Acknowledgements

I am grateful to Dr Howard Roe (Institute of Oceanographic Sciences) for arranging the loan of this material and for providing other relevant data. I would also like to thank Dr Roger Lincoln for reading and commenting on the manuscript and Miss Ann Gurney for her help in the preparation of the manuscript. Dr Brigitte Volkmann (Istituto di Biologia del Mare, Venezia) examined some of the tisbid material and I am very grateful for her detailed comments and advice. I would also like to thank Dr G. Deevey for allowing me to examine her specimen of *Bathyidia remota*.

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Manuscript accepted for publication 20 March 1978

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Bulletin of the
British Museum (Natural History)

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Zoology series Vol 35 No 4 31 May 1979

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

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ISSN 0007–1498

Zoology series
Vol 35 No 4 pp 265–322

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 31 May 1979

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Part I.

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Introduction

As currently recognized, the genus *Haplochromis* Hilgendorf encompasses over 300 species, some doubtless nominal but the majority of apparent biological validity (see Fryer & Iles, 1972; Greenwood, 1974*a*). It is the most speciose African taxon in the family Cichlidae and, next to the genus *Sarotherodon* has the widest distribution in the continent, extending from Tunisia in the north to Namibia (South West Africa) in the south. It is, however, virtually absent from west Africa, being represented there by only one or two species from Nigeria.

Amongst its numbers, indeed contributing the greatest number of species, are the well-known *Haplochromis* flocks of Lakes Victoria and Malawi (Trewavas, 1935; Fryer & Iles, 1972; Greenwood, 1974*a*), together with the smaller and less studied flocks of Lakes Edward, George, Turkana (Rudolf), Albert and Kivu (see Regan, 1921*a*; Poll, 1932; Trewavas, 1933; Trewavas, 1938; Greenwood, 1973, 1974*b*).

It is amongst the species of these various lacustrine flocks that one encounters the great range of anatomical, dental and morphological differentiation usually associated with the genus. The fluviatile species appear to be less diversified, but even here there is more diversity than is realized at first.

With this wide range of anatomical and morphological variation it is not surprising that the present concept of the genus, both in morphological and in phyletic terms, is very ill-defined. Indeed, the concept of *Haplochromis* seems to be based entirely on some intuitive appreciation of 'overall similarity' amongst its constituent species. There has been, so far, no real attempt to test the validity of the implicit monophyly of these species. The recognizable and often noted intrageneric variability in *Haplochromis* has, until recently, not been seen as an analytical taxonomic tool because thinking amongst systematists working on cichlids has been dominated by a 'size of the morphological gap' approach to supraspecific classification.

A reappraisal of the situation with this variation seen in terms of derived (apomorph) and primitive (pleisomorph) character states has not been applied to the genus as a whole (but see Greenwood, 1974*a*, for the Lake Victoria species). It is this basically Hennigian approach (Hennig, 1966) that I have attempted to apply to the problem. Its use, I believe, does allow one to produce a more realistic classification of the species now lumped together in *Haplochromis*, or separated from that genus because of their showing an extreme manifestation of features already indicated in species still retained in *Haplochromis*.

The taxon *Haplochromis* was first introduced by Hilgendorf (1888), as a subgenus of *Chromis*, for his new species aptly named '*obliquidens*' (see Greenwood, 1956*a*). The fine, closely packed and multiseriate teeth of '*obliquidens*', with their protracted and obliquely truncate crowns (see Fig. 7B), provided the diagnostic features for Hilgendorf's subgenus.

No further species were added to *Haplochromis* until Boulenger (1906) elevated the taxon to generic rank and included in it six new species from Lake Victoria and the Victoria Nile. Boulenger gave no reasons for raising Hilgendorf's subgenus to a full genus, nor did he attempt to define *Haplochromis* so as to accommodate the new species, none of which had teeth like those of

H. obliquidens. A footnote to the paper (Boulenger, 1906 : 443) might be interpreted as a generic definition, but it is completely inadequate and rather confusing, merely noting that '. . . in addition to the character of the dentition, intermediate between *Paratilapia* and *Tilapia*, the fishes of this genus differ from the latter in usually having a considerable portion of the maxillary bone exposed when the mouth is fully closed'.

The following year Boulenger (1907 : 495) did provide a formal definition of *Haplochromis*, in which genus he then synonymized Pffefer's (1893) genus *Ctenochromis* and Pellegrin's (1903) *Astatoreochromis* (now recognized as a distinct genus, see Greenwood, 1959*a*; Poll, 1974 and p. 285 below). This definition is, however, very vague and so worded that it is impossible to distinguish Boulenger's concept of *Haplochromis* from that of his redefined *Paratilapia* Bleeker.

The situation remained virtually unchanged, except for the addition of several more species, with the publication of the third volume in Boulenger's *Catalogue of African Freshwater Fishes* (1915) in which he again comments that some *Haplochromis* species '. . . vary to such an extent in their dentition that [they] might be referred to *Tilapia* and others to *Paratilapia*'.

Regan's (1920, 1922*a*) fundamental studies on the osteology of African Cichlidae, and his consequent revision of Boulenger's genera, resulted in many more species being included in *Haplochromis* (which then became the '. . . largest African genus', Regan, 1920 : 45). In his 1920 paper Regan also defined (in a footnote) several genera which, although apparently related to *Haplochromis*, differed from that genus in various dental features, both oral and pharyngeal.

Surprisingly, in the light of these other generic definitions, Regan was content to include in *Haplochromis* a majority of species whose dental characters were quite unlike those of the type species. In effect, Regan's redefinition of *Haplochromis* in these and subsequent papers (especially those of 1921*a* & *b* and 1922*a* & *b*) was only a slight improvement of that provided by Boulenger. *Haplochromis* remained a polymorphous assemblage of species showing a wide range of dental and other anatomical peculiarities, only united by having a particular kind of cranial apophysis for the upper pharyngeal bones. Since a similar apophysis occurs in other taxa defined by Regan, the monophyletic origin of *Hapolchromis* was not established.

That Regan was aware of his system's shortcomings is shown by remarks in his papers on the cichlids of Lakes Malawi (1921*b*) and Victoria (1922*b*). For example, regarding the *Haplochromis* of Lake Victoria he wrote (Regan, 1922*b* : 158): 'The species of *Haplochromis* exhibit almost as great a diversity as in Nyassa, yet there are certain features which enable one to say almost at a glance to which lake a species belongs', and on page 160: 'From what has been said above as to the evolution and relationships of the Cichlidae of Victoria, it will be evident that I do not regard the classification here proposed as entirely satisfactory'.

Regarding the species of Lake Malawi, Regan (1921*b* : 686) has this to say: '. . . the absence of evident relationship to species found elsewhere leads to the conclusion that the Nyassa species are a natural group and may, perhaps, have evolved in the lake from a single ancestral form'. Regrettably, Regan does not elaborate on his remark about the absence of evident relationship to species found elsewhere, particularly since a year later he was to place the majority of Lake Victoria species in the same genus.

When revising the Lake Victoria species, Regan (1922*b*) divided the *Haplochromis* into five subgenera, *Neochromis* for *H. nigricans* and *H. nuchisquamulatus*, *Bayonia* for *H. xenodon* (now considered a synonym of *Macropleurodus*, see Greenwood, 1956*b*), *Haplochromis* for *H. obliquidens*, and *Ctenochromis* for the remaining 42 species. These latter were characterized by their having conical or bicuspid teeth separated by an interspace from the smaller inner teeth, the other subgenera having variously specialized crown forms to the teeth. Regan disregarded, or perhaps failed to appreciate the principal diagnostic feature which Pfeffer (1893) used to diagnose *Ctenochromis*, namely the very small scales on the thoracic region. Both Pfeffer and Regan overlooked other diagnostic features in *Ctenochromis pectoralis* (type species of the genus), none of which is found in any of the 42 Victoria species placed in Regan's *Ctenochromis* subdivision of that flock (see p. 287 below). Recent research (summarized in Greenwood, 1974*a*) also indicates that these 42 species, and about an equal number described since Regan's 1922 revision, can be subdivided into several distinct groups.

Similar arguments can be marshalled against Regan's (1922*a* : 253) statement that '. . . the species (of *Haplochromis*) not peculiar to the Great Lakes all belong to the subgenus *Ctenochromis*, Pfeffer . . .'; this aspect of the problem will be discussed later.

Since Regan's time, no real attempts have been made to subdivide the genus (which now contains almost double the number of species known to Regan). Some species have been separated off as mono- or oligotypic genera, but these actions have in no way simplified the problem either taxonomically or phylogenetically, and the genus has still not been shown to be a monophyletic unit.

Clearly, to test the phylogenetic integrity of such a large, ill-defined taxon will require much detailed and critical analysis. The present paper must be looked upon as a tentative first step in that direction. I shall limit my detailed analysis to those *Haplochromis* species which I have studied in some depth, *viz.* the species flock of Lake Victoria (which contains the type species, *H. obliquidens*) and those of Lakes Turkana, Albert, Edward and George, together with the few *Haplochromis* occurring in Lake Tanganyika, and the purely fluviatile species from Africa and the Middle East. Also included are the *Haplochromis*-like riverine genera *Orthochromis* Greenwood, *Serranochromis* Regan and *Rheohaplochromis* Thys van den Audenaerde, and the partly lacustrine *Astatoreochromis* Pellegrin. Unfortunately, I have been unable, through lack of first-hand knowledge, to include the Lake Malawi *Haplochromis* flock. However, I trust that the results of my analysis of these other *Haplochromis* species will enable workers on the Malawi fishes to review the species of that lake in a new light.

My review of anatomical, osteological and morphological features, including details of secondary sexual markings and coloration, has yielded one particularly significant (but not surprising) result; there is, apparently, not one derived feature shared only by the 190 species examined.

The commonly occurring tooth form, an unequally bicuspid tooth, is found in several other genera, as is the unicuspid and caniniform type. Even some of the specialized dental types seem to have evolved independently in other genera, these genera, and those in which bi- and unicuspid teeth also occur, each being recognizable on the basis of derived features not shared by *Haplochromis*.

The structure of the cranial apophysis for the upper pharyngeal bones (see Regan, 1920) is probably a derived feature (see Greenwood, 1978), but again it is a feature widely distributed amongst several genera whose close affinity with *Haplochromis* cannot be established. At best the pharyngeal apophysis can be used as an indicator of relationship at a more distant level than the 'generic' one (see Greenwood, 1978).

No derived features of the anatomy or the squamation are universally shared amongst all the species although, as with various other characters, distinct groups can be defined within *Haplochromis* on the basis of shared derived features.

The anal fin markings found in adult male *Haplochromis*, the so-called anal ocelli or egg-dummies (see Wickler, 1962*a* & *b*; Trewavas, 1973), have been considered a unique feature of the genus. Trewavas (1973 : 34) expressed the generally held view on these markings when she wrote '. . . within their endless diversity the species of *Haplochromis* have almost universally in common a feature of the colour-pattern, the well-known *ocellar spots* on the anal fin of the male' (italics mine). Certainly such ocellar markings are present in all the described species of *Haplochromis* from Lake Victoria, Edward, George and Kivu, and probably in those from Lake Turkana as well. But, true ocelli (i.e. a central coloured spot with a clear surround) are not found in the species of Lake Albert, in the majority of species occurring in the rivers, nor even in many of the Lake Malawi species (see figs in Axelrod & Burgess, 1977). Coloured markings do occur on the anal fins of these fishes (sometimes in both sexes), but are in the form of spots without a clear surround, often smaller than the true ocellar type, sometimes more numerous and covering the greater part of the fin, sometimes only as one or two spots, or, less commonly, similar in number (3–5) and linear arrangements to the true ocellar type.

Clearly, the presence of ocellar anal markings cannot be considered a character of *Haplochromis* as that genus is currently conceived, and the value of anal markings *per se* as an indicator of phyletic relationship must be reassessed.

Although a monophyletic origin for the 'genus' *Haplochromis* cannot be established, it is possible to recognize several seemingly monophyletic lineages (reconstructed on the basis of synapomorphic characters) amongst the species of Lake Victoria (Greenwood, 1974*a* and unpublished). None of the six major lineages recognized in that lake, however, could be interrelated on a sister-group basis (although sister-groups could be recognized within five of the lineages themselves). In other words, the synapomorphic features of each lineage are superimposed on a basic, plesiomorphic 'bauplan' shared by all*.

A similar picture emerges when the fluviatile species, and those from Lakes Albert, Turkana and Tanganyika are examined closely. That is, one can postulate a number of lineages (some containing both fluviatile and lacustrine members), but none can be further interrelated on the basis of synapomorphic features.

With the possible exception of their occurrence in two species (one from Lake Victoria, the other from Lake George), none of the apomorph features used to delineate these lineages has been observed amongst the '*Haplochromis*' species of Lakes Victoria, Edward, George and Kivu.

Although no apomorph character has been found to unite all the species of Lakes Victoria, Edward, George and Kivu, and thus suggest their common ancestry, species from the different lakes can be grouped into common lineages each of presumed monophyletic origin. For that reason the '*Haplochromis*' of Lakes Edward, Kivu and George will be treated together with those of Victoria in a forthcoming paper (except for those species which are now referred to the redefined genus *Haplochromis*, see p. 280).

To summarize, the so-called *Haplochromis* species of Africa (excepting those of Lake Malawi which are not included in this review) can be split into a number of major lineages. Most of these lineages are characterized by derived features unique to its members.

The different lineages cannot be interrelated on a sister-group basis for want of ascertainable synapomorphic features which would permit the recognition of their sister-group status. I use the qualification 'most of these' because one of the groups cannot be defined on the basis of even a single shared apomorph character. This is the group in which must be placed the widespread *H. bloyeti* species complex of east Africa (see Greenwood, 1971, 1974*a*) and, probably, certain of the generalized endemic species of Lake Victoria, Edward and Kivu; it is recognized merely on the overall similarity (and plesiomorphy) of its constituent species.

Wherever breeding habits are known, members of the various lineages described in this paper are female mouth brooders, and all have a '*Haplochromis*'-type cranial apophysis for the upper pharyngeal bones (Greenwood, 1978), features shared with the '*Haplochromis*' and several seemingly related species in Lake Malawi (Trewavas, 1935; Greenwood, 1978). Oral brooding and its associated spawning behaviour, as compared with substrate spawning and brood-care, is a derived condition; the '*Haplochromis*'-type apophysis would also seem to be a derived feature. One may therefore hypothesize a shared common ancestry, at some point, both for the lineages described below and for those which eventually will be recognized amongst the Lake Malawi haplochromine species (i.e. those with a '*Haplochromis*'-type pharyngeal apophysis and, probably species with a '*Tropheus*'-type apophysis as well; see Greenwood, 1978).

For the moment, however, and until it is possible to interrelate dichotomously the various lineages on a sister-group basis, one is faced with a series of unresolved dichotomies (see, for example, the problem discussed on p. 313). In classifying this assemblage I have followed the convention suggested by Nelson (1972), namely that the taxa (i.e. the individual lineages) be given equal rank. At this stage in our knowledge of supraspecific relationships amongst African cichlids, generic rank would seem to be the most appropriate.

Methods and materials

Methods

In essence I have attempted to break up the 'genus' *Haplochromis* into a number of monophyletic lineages, the members of each lineage being related by their relative recency of common ancestry. Recency of common ancestry, in turn, is recognized by members of a lineage possessing derived (apomorph) characters which are not shared with other species.

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* It has been assumed (on the basis of overall morphological similarity between the least specialized members of each lineage) that the endemic *Haplochromis* species of Lake Victoria are of monophyletic origin (Greenwood, 1974*a*). Since no apomorph feature unique to the Victoria species has yet been found, that hypothesis is without formal support.

Determining the primitive (plesiomorph) or derived status of characters in the Cichlidae is at present a very difficult task. No guidance is available from the entirely inadequate fossil record, and the family's nearest living relatives have yet to be recognized. Comparisons between different character states (outgroup comparison, see Hecht & Edwards, 1977) ideally should be carried out across the whole family. As there are well over 600 nominal species in Africa and America, few of which have been studied in the detail necessary for proper phyletic analysis, the level of outgroup comparisons employed in this paper is, perforce, a low one.

All comparisons have been restricted to African taxa, in particular to species and lineages within the group having a '*Haplochromis*'-type of pharyngeal apophysis. This decision was made on the assumption that all such taxa were derived from a common ancestor, albeit a distant one, and that the '*Haplochromis*'-type apophysis, relative to the '*Tilapia*'-type, is itself a derived character. The most detailed comparisons, of course, have been those made between species comprising the lineages discussed in this paper.

Outgroup comparisons have also been made with species having a '*Tilapia*'-type apophysis, in particular the lineages represented by the genera *Sarotherodon* and *Tilapia.*

When comparisons were made with *Haplochromis* from Lake Victoria, the Victorian lineages were those discussed in Greenwood (1974*a*). Since no such breakdown is available for the endemic *Haplochromis* of Lake Malawi or for the endemic genera with a '*Haplochromis*'-type apophysis in Lake Tanganyika, these various taxa were not involved in the analysis.

The particular characters and character transformations studied are those which, after a preliminary survey of the taxa involved*, seemed to be most likely to yield information on their derived or primitive states within the material available and within the limits of the tests which could be applied to the conclusions reached.

As might be expected, the principal test was that of the distribution of a character state amongst the species compared. The state having the widest occurrence is assumed to be the most primitive one, that with the most circumscribed distribution the derived one (the so-called commonality principle of Schaeffer, Hecht & Eldredge, 1972).

The characters finally selected, and a few others that deserve comment, can now be discussed.

(*i*) *Squamation.* All *Haplochromis* have the scales on the chest region (the area anterior to a line through the pelvic and pectoral fin insertions, and ventral to a horizontal line through the ventral part of the pectoral fin insertion) smaller than those on the ventral and ventrolateral parts of the body. The common condition is that in which the size change between the scales of the two regions is a gradual one, see Fig. 1; even when, as in *H. squamulatus* of Lake Victoria, the chest scales are noticeably small, the size change is still gradual (see fig. 17 in Greenwood, 1967). The less frequent condition is that in which the size transition (usually along the line between pectoral and pelvic fin insertions, but sometimes a little further posteriorly) is abrupt; since in these fishes the chest scales are generally small and numerous, the chest squamation is noticeably distinct from that of the belly and ventral flank regions (Figs 2 & 3).

A totally scaled chest, irrespective of squamation pattern, is the usual condition; circumscribed, bilaterally symmetrical naked patches are uncommon and are confined to species showing an abrupt size transition in thoracic-abdominal scale sizes. A completely naked chest is the most uncommon condition and would seem to be the end point in the apomorphic morphocline: abrupt size change ➛ bilateral naked patches ➛ completely naked chest.

Although the ventral body scales extending posteriorly from the pelvic fin insertions to the anus are smaller than those on the lateral and ventrolateral aspects of the flanks, the size gradation between the two fields is generally gradual. However, in a few species the ventral (belly) scales are much reduced in size and thus are clearly demarcated from the flank scales above them. This condition is correlated with an equally marked and abrupt size reduction in the scales on the chest, so that the tiny abdominal scales appear as a posterior and ventrolateral extension of those on the chest (Fig. 3). Such an arrangement is also considered to be a derived condition.

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* The *Haplochromis* species of Lakes Victoria, Albert, Turkana, Tangaṅyika, Edward, George and Kivu, of the African rivers and those of Syria and Israel, and the species of *Serranochromis, Rheohaplochromis, Orthochromis, Astatoreochromis, Macropleurodus, Platytaeniodus* and *Hoplotilapia*, a total of some 390 species.

Surprisingly, in a group of species where most morphological features appear as elements in a continuum of differentiation, the various scale patterns discussed above are very trenchantly separated from one another. The few intermediate specimens I have observed are clearly individual rather than populational or specific variants.

As with the chest, a completely scaled cheek is the common condition, the scales being arranged in three or four horizontal rows. Reduced squamation is encountered infrequently, but ranges from a narrow naked band (one or two rows deep) along the ventral margin, to an almost completely naked cheek with only the suborbital row, or part of that row, persisting.

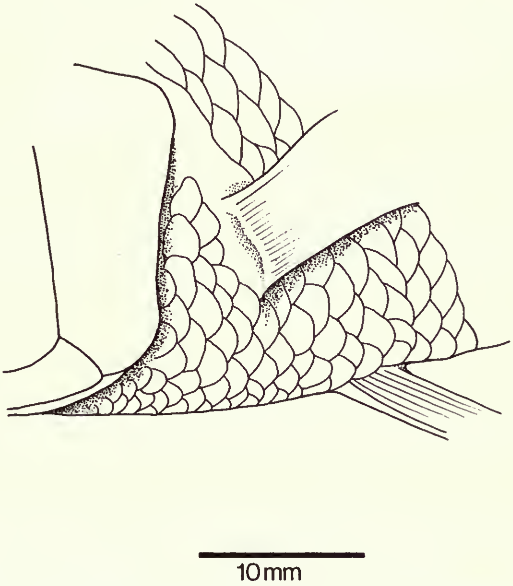

Fig. 1 Thoracic-abdominal scale transition in *Astatotilapia nubila*; left lateral view.

On the principle of commonality (Schaeffer *et al*, 1972), strongly ctenoid body scales should be looked upon as the primitive condition, and an increase in the area of the body covered by cycloid or reduced ctenoid scales should be considered the derived one*.

Some uncertainty about this conclusion could be raised by the situation in *Hemichromis*, also a '*Haplochromis*' group species (see Regan, 1922*a*). Here the scales are mostly cycloid with a few weakly ctenoid ones confined to the anterior part of the body; that is, a presumably derived condition. But *Hemichromis* species are substrate spawners and brood guarders, a presumed primitive condition amongst African cichlids. Since certain other characters in *Hemichromis* are apparently derived ones (the unicuspid outer teeth, the number of inner tooth rows (one or none), and the form of the upper jaw), the cycloid scales may have evolved independently in the lineage. On the other hand, the presence of cycloid scales in '*Tilapia*' group species (see footnote), some of which are also substrate spawners and all of which have an apparently plesiomorph type of pharyngeal apophysis (see Greenwood, 1978), would appear to strengthen the argument for considering cycloid scales as primitive features. In the face of such contradictory observations it would seem advisable not to use this type of scale ornamentation in phyletic analysis.

All the *Haplochromis* and *Haplochromis* group species used in this review (see footnote p. 270) have less than the proximal two-thirds of the caudal fin covered by small scales; usually only the

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* Most taxa in the '*Tilapia*' group, as defined by apophyseal structure (see Greenwood, 1978), have cycloid scales, although some have a few weakly ctenoid scales on the anterior part of the body).

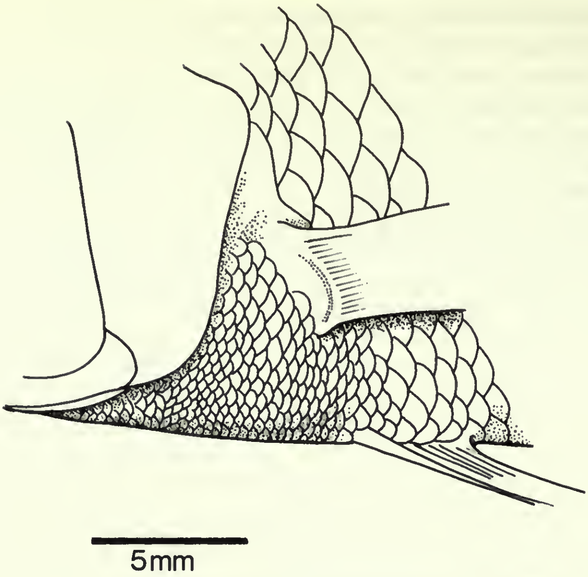

Fig. 2 Thoracic-abdominal scale transition in *Thoracochromis wingatii*; left lateral view.

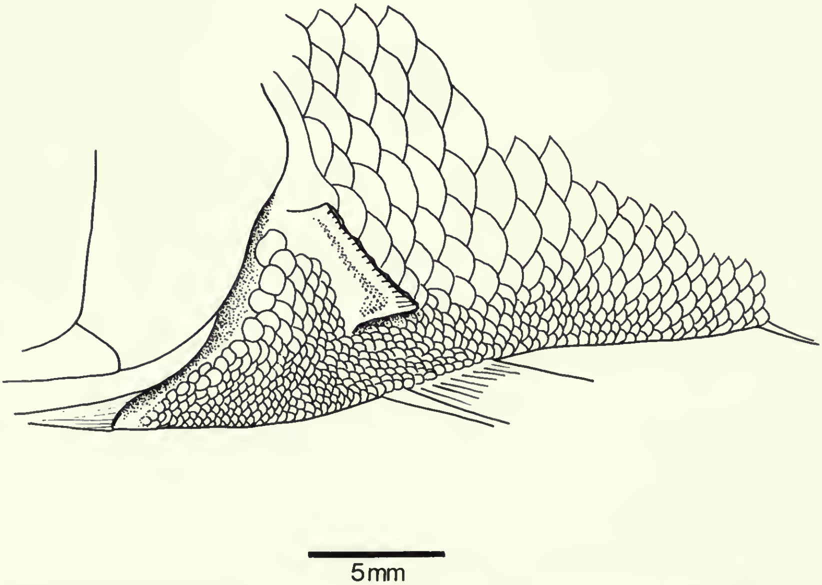

Fig. 3 Thoracic–abdominal scale transition in *Orthochromis polyacanthus*; left lateral view.

proximal half is covered. In contrast, all the endemic lacustrine species from Lake Malawi have the entire fin densely scaled (Trewavas, 1935). The partly scaled condition is assumed to be the plesiomorph one.

(*ii*) *Dentition*. Outer tooth row in both jaws. The most frequently occurring tooth form (Fig. 4) is that with an unequally bicuspid crown, moderately distinct neck and relatively stout body firmly attached to the underlying bone. Neither cusp is strongly compressed, their tips are acute or subacute and lie in or but slightly outside a vertical drawn through the corresponding outer margin of the tooth's body. Such teeth, apart from providing the definitive dental form in many species, also precede the definitive tooth type in species having unicuspid teeth in adult fishes, and also, in at least some species, precede the definitive types when these are much modified versions of the basic bicuspid (e.g. in *H. obliquidens*). Unfortunately, ontogenetic data on tooth replacement are not available for many species, so the generality of the latter observation is unknown.

Because of its common occurrence and its primary position in the ontogenetic sequence of tooth replacement, the unequally bicuspid tooth is taken to be the plesiomorph dental type. Bicuspid teeth in which there is a differential growth of one cusp (usually the larger one) or equal development of both cusps are considered to be derived features, as are unicuspid teeth.

As mentioned above, most taxa having a definitive outer row dentition composed of unicuspid teeth also have an ontogenetically earlier one of bicuspids (usually persisting until an individual fish is between 80 and 100 mm standard length). Any shift forward in the time or body size at which the definitive unicuspid teeth appear can therefore be interpreted as being a derived condition.

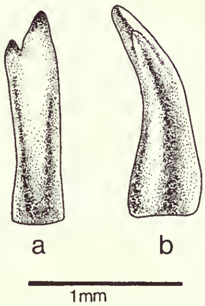

Fig. 4 Outer row jaw teeth (premaxillary) of *Astatotilapia flaviijosephi*. A. Labial view. B. Lateral view (posterior aspect).

From one to six (rarely as many as twelve) enlarged and unicuspid teeth occur posteriorly on the premaxilla, even when the other teeth on that bone are bicuspids. The replacement of these unicuspids by teeth similar to those on the rest of the premaxilla must be considered a derived condition.

Inner row teeth. Here, on the grounds of common occurrence, small, tricuspid teeth must represent the primitive condition. As with the outer teeth, there can be an ontogenetic succession of teeth types, tricuspids or a mixture of tri- and bicuspids preceding unicuspids. Occasionally some or all inner rows are composed of highly modified bicuspid types resembling, albeit on a smaller scale, those of the outer row (e.g. *Haplochromis obliquidens* and *Macropleurodus bicolor*; see Greenwood, 1974*a*).

The presence of inner teeth other than tricuspids is a derived condition. Since most commonly there are from 2 to 3 rows of inner teeth, any increase or decrease in the number of rows must also indicate an apomorph condition.

(*iii*) *The lower pharyngeal bone and its dentition.* The most commonly encountered form of lower pharyngeal bone has an approximately equilateral, triangular dentigerous surface, is not noticeably thickened or robust, and has its anterior blade-like portion neither noticeably elongate nor short (Fig. 5).

The teeth are arranged anteroposteriorly in about 30 to 50 rows, with those in the two median and in the posterior transverse row stouter than the others but, like them, retaining an unequally bicuspid crown in which the minor cusp is a near horizontal shoulder and the major one is weakly falciform and vertically aligned.

Apomorphic derivations from this basic type include changes in overall outline shape of the dentigerous area (Fig. 14), elongation of the anterior blade, increase or decrease in the number of tooth rows, an increase or, less commonly, a decrease in the number of rows of coarser teeth

(Figs 20 & 8), and changes in crown morphology of the teeth (generally a process of molarization associated with a general coarsening of tooth form; see Fig. 18B).

(*iv*) *Neurocranial morphology*. Modal neurocranial form (and thus the presumed plesiomorph condition) is best appreciated from a drawing (Fig. 6).

Salient features are the moderately high supraoccipital crest (*c*. three-quarters of the depth of the otic skull region measured from roof to ventral parasphenoidal face, but excluding the pharyngeal apophysis); the preorbital skull profile (from vomerine tip to the anterior point of the supraoccipital crest) rising at an angle of *c*.45°, its outline gently curved and its ethmovomerine region sloping forwards and downwards at a slight angle; the preotic part of the skull (measured from the vomerine tip to the anterior vertical wall of the prootic bone) comprising some 55–60% of the total length of the neurocranium, and the otic region of the skull not inflated. The pharyngeal apophysis is not enlarged, and the prootic does not contribute to the articular surface (Greenwood, 1978).

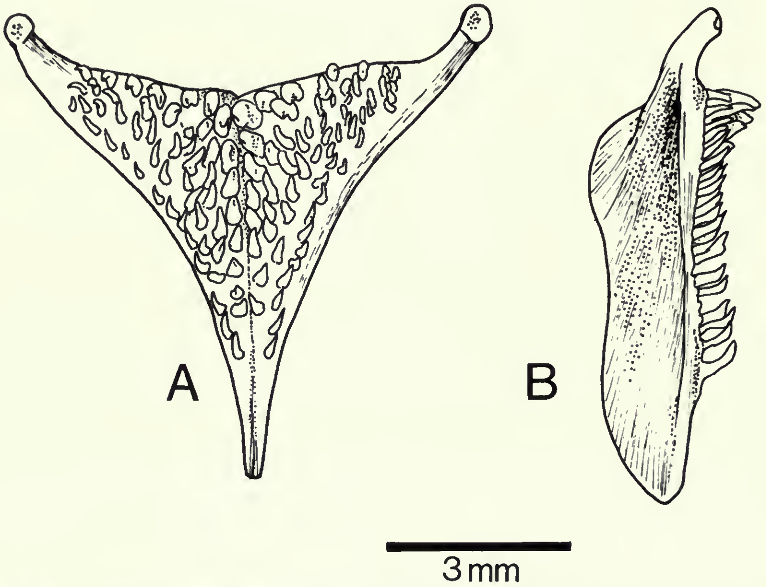

Fig. 5 Lower pharyngeal bone of *Astatotilapia bloyeti*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

Derivative conditions include elongation of the preotic part of the skull (to about 70% of the neurocranial length) correlated with a flattening of the preorbital skull profile (Fig. 13); narrowing of the otic region, and in some variants a relative lowering of the supraoccipital crest; the retention of a basic skull form in the otic region but a marked increase in the slope of the ethmovomerine region (in some species almost to the vertical) and a correlated increase in the slope and curvature of the preorbital skull profile; the retention of basic otic and ethmovomerine regions but the elevation of the preorbital skull roof so that the neurocranium becomes higher and more angular in outline (see Greenwood, 1974*a*, for further analysis and figures).

Departure from the plesiomorph condition for the pharyngeal apophysis is always associated with an hypertrophy of the upper and lower pharyngeal bones and their dentition (see Greenwood, 1965*a*, 1974*a*, 1978).

(*v*) *Anal fin markings* (*egg-dummies*) *in male fishes*. Reference has already been made (p. 268) to the variety of these markings in *Haplochromis*. (See Wickler, 1962*a* & *b*, 1963 for a discussion of their importance in the breeding biology of these fishes).

Regrettably there is little information about these markings in live fishes, and what has been recorded is often insufficiently detailed to be of value. For instance, it is important to know if the markings are merely coloured spots, whether each spot has a contrasting border, or whether it is truly an ocellus with a wide and translucent surround. The number and distribution of the markings are also important data. My own observations on live fishes from different parts of Africa, and on preserved material as well, all suggest that the anal markings (or their absence) may be of considerable value in helping to define lineages. But, because of a paucity of information for many species considered below it has proved impossible to use the character fully in this study.

It seems reasonable to assume that the egg-dummy markings (using that term in its widest sense and not just for true ocelli) were derived from coloured streaks and spots like those that are an almost universal feature on the dorsal fins of cichlids (see Wickler, 1962*a*). The first steps in the evolution of egg-dummies from a maculate colour pattern would involve a slight reduction in the number of spots and a consequent increase in the space between them, and the intensification or alteration of their colour so as to differentiate the anal spots from those in the dorsal fin. The end point in this process of differentiation seemingly would be reached with the development of ocellar spots.

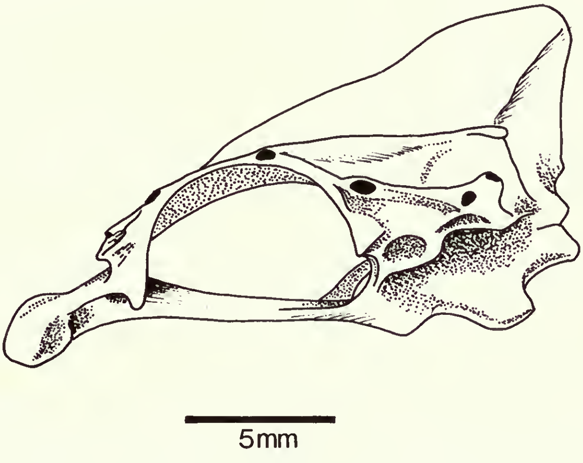

Fig. 6 Neurocranium of *Astatotilapia bloyeti*; left lateral view.

In species with true ocellar egg-dummies (e.g. the *Haplochromis* of Lake Victoria; see Greenwood, 1974*a*, especially plate I) the number of spots is reduced to modes of 3 or 4, the coloured centre of each spot is ovoid in outline, generally has a narrow black or dark border and is surrounded by a clear zone of fin membrane; other spots and markings on the fin are suppressed, although the greater part of the fin may have a coloured flush. The result is a most distinctive mark, with an illusion of three dimensionality, that is readily distinguished from any other fin or body markings.

There are, of course, other kinds of anal marking which, in their appearance, size and distribution on the fin, are intermediate between the supposed plesiomorph type (numerous, nonocellate spots) and the presumed apomorph kind described in the last paragraph. Their possible phylogenetic importance will become apparent when more information is available not only on their appearance in live animals, but also on their functional role in mate recognition, courtship and spawning.

For the moment one can assume that the ocellar spots represent the apomorph condition and that the multiple spot type of anal marking is the plesiomorph one. Those *Haplochromis*-like species apparently without any spatially or chromatically differentiated anal markings (e.g. *Orthochromis malagaraziensis*; Greenwood, 1954) provide a particular problem because we know nothing of their reproductive behaviour. Thus the absence of 'egg-dummies' cannot necessarily be construed as representing a plesiomorph condition in these species.

(*vi*) *Vertebral numbers.* The modal range of total vertebral counts (excluding the fused $PU_1 + U_1$ urostylar element) is 27–29 (comprising 12–14 abdominal and 15 or 16 caudal centra). On the grounds of its being the modal number, it is taken to be the plesiomorph condition.

Apomorphic deviations occur amongst the *Haplochromis* species of Lake Victoria where a few species show a higher modal count (30–32); these are all long-bodied piscivorous predators and the increase in the number of vertebrae occurs in the caudal section of the column. Parenthetically, it may be noted that Lake Malawi *Haplochromis* species with more than 32 vertebrae also show an increase in the number of caudal elements.

The most marked increase in vertebral numbers (apart from that in some Malawi species) is found in the genus *Serranochromis.* Here the modal counts are 33 and 34 (abdominal modes 16–17, caudal modes also 16 and 17), with an increase in the number of abdominal rather than the caudal elements as was the situation in the Victoria and Malawi *Haplochromis* species.

A similar increase in the number of abdominal vertebrae is also found in the seven Zambezi species of so-called *Haplochromis* revised by Bell-Cross (1975). In these species there is, however, a reduction in the number of caudal vertebrae as compared both with *Serranochromis* and with the plesiomorphic *Haplochromis* condition (14 and 15 in the Zambezi species, 16 and 17 in the others). In consequence, the modal total count (29–32) for the Zambezi fishes overlaps that of the plesiomorph *Haplochromis* type.

For want of falsifying evidence, the *Serranochromis* and 'Zambezi *Haplochromis*' conditions are both considered to be apomorphic ones.

In some *Haplochromis*-like genera, certain species have low counts for caudal vertebrae, but modal ones for the abdominal elements (see p. 290); probably these taxa, in the phyletic context of their particular lineages (and for this particular character), should be considered derived (i.e. autapomorphic).

(*vii*) *Caudal fin skeleton.* Vandewalle (1973) has provided a summary of the caudal fin skeleton in 108 cichlid species, mostly African. He shows that, overall, there is a remarkable constancy in this feature but that in some species individual hypural elements may fuse (especially hypural 1 with 2, and 3 with 4; the fifth hypural is always free except in one species (see p. 292) – Vandewalle finds no instance of fusion between all hypurals).

My own observations generally confirm those of Vandewalle, but strongly indicate that, with one possibly exceptional lineage (see p. 297), hypural fusion is an individual and not a specific or lineage trait. It is thus of very restricted value as an indicator of phyletic affinities, as is the organization of the whole caudal fin skeleton amongst the taxa examined.

(*viii*) *Number of dorsal and anal fin rays.* Amongst the *Haplochromis* species and related taxa reviewed (see footnote p. 270) the modal numbers of dorsal fin rays are 15 and 16, and of branched rays 9 and 10. Except for obvious individual variants, and two species of *Astatoreochromis*, all these taxa have 3 spinous rays in the anal fin and, modally, 8 or 9 branched rays.

If, on the principle of commonality, these numbers are taken to be the basic (i.e. plesiomorph) counts, then modal ray counts for either fin that are higher or lower should be considered derived features.

(*ix*) *Gill rakers.* There is a fairly narrow range of both gill raker numbers and shapes (counts and observations restricted to the outer row of gill rakers on the lower part of the first gill arch). In most species the rakers are relatively robust, simple structures (with sometimes the upper 2 or 3 of the series flattened and bi-, tri- or even polyfid), of moderate length and numbering from 7 to 12 (modal counts 8 and 9).

Materials

All the BMNH material (spirit specimens, alizarin preparations, dry skeletons and radiographs) of all the taxa named in this paper has been examined, as have the Museum's collections of *Haplochromis* species from Lakes Victoria, Edward, George and Kivu, and selected specimens from the collection of Lake Malawi *Haplochromis* species and related genera.

In addition, the following specimens, borrowed from other institutions, have also been studied (and radiographed).

Haplochromis albolabris	(Holotype)	H1784
Haplochromis angusticeps		ANSP 54369–76
Haplochromis bakongo	(Paratypes)	RMAC 16945–947
Haplochromis buysi	(Holotype)	WH P1219
Haplochromis darlingi		AM/P2461
Haplochromis fasciatus		RMAC 48407–415
Haplochromis giardi	(Holotype)	MHN A2754
Haplochromis luluae	(Paratypes)	ANSP 51759–62
Haplochromis oligacanthus		RMAC 167930–931
Haplochromis polli	(Paratypes)	RMAC 99403–404
Haplochromis stappersi		RMAC uncatalogued
Haplochromis thysi	(Holotype)	RMAC 163991
Haplochromis toddi	(Holotype)	RMAC 1346
Haplochromis torrenticola		IRSN 1809–1960
Chetia brevis	(Holotype)	AM/P951
Chetia brevis	(Paratypes)	AM/P952
Chetia brevis		AM/P1425–6
Chetia flaviventris		AM/P1298
Ctenochromis pectoralis	(Lectotype)	ZMH402
Ctenochromis pectoralis	(Paratypes)	ZMH403

AM/P, Albany Museum; ANSP, Academy of Natural Sciences of Philadelphia; IRSN, Institut Royal des Sciences Naturelles de Belgique; H, Zoologisches Museum, Hamburg; MNH, Museum National d'Histoire Naturelle, Paris; RMAC, Musee Royal de l'Afrique Centrale, Tervuren; WH, Windhoek Museum; ZMH, Zoologisches Museum, Berlin.

Classification

Applying the methodology and reasoning discussed above and in the Introduction, nine lineages, here given generic rank, may be recognized amongst the taxa studied. With the exception only of *Chetia*, each of these genera now contains species that were previously placed in *Haplochromis*.

Unless indicated otherwise, all the genera have a cranial apophysis for the upper pharyngeal bones formed from the parasphenoid and basioccipital (see '*Haplochromis*'-type apophysis in Greenwood, 1978) and a caudal fin scaled on its proximal half or less.

All vertebral counts quoted exclude the fused PU_1 and U_1 centra, and may thus be lower than those used by some other authors; abdominal vertebrae are identified as those bearing pleural ribs (including, of course, the first two vertebrae that have no ribs), and the caudal centra as those without ribs but, except occasionally the first (anterior) centrum, with a haemal arch.

Since the genus *Haplochromis* is now restricted to five species (see p. 280), difficulties arise when reference is made either to species formerly included in that genus, but which have not yet been assigned to other genera, or to the former concept of the genus *Haplochromis*. To avoid confusion, I have adopted the convention proposed and used by Patterson & Rosen (1977 : 163) for dealing with such situations. Namely, to prefix the species name with its former generic name cited between quotation marks, i.e. '*Haplochromis*' *nigricans* or '*H*' *nigricans*. When reference is made to the former concept of the genus the generic name alone, but in quotation marks, is used.

The Lake Victoria '*Haplochromis*' species will be reviewed in a paper now in preparation; until its publication these species can be referred to by using the old generic name in quotes. As a temporary expedient for general use until such times as the Lake Malawi '*Haplochromis*' are revised, a purely formal generic name for these species is proposed on p. 317.

Species mentioned in this paper are listed in the index on p. 321 under their former generic names (usually *Haplochromis*), with a reference first to the page on which they are listed in their new generic grouping, and secondly to the page on which that genus is described.

In the generic descriptions, presumed apomorph (i.e. derived) character states are italicized.

The generic revision which follows is arranged in two parts. After redefining the genus *Haplochromis* Hilgendorf, 1888, the first section will deal with '*Haplochromis*' species from Lakes Turkana, Albert, Tanganyika and Mweru, and with those from the Nile and Zaire river drainage systems, and the rivers of Kenya, Uganda and Tanzania.

The genera *Orthochromis* Greenwood, 1954, and *Astatoreochromis* Pellegrin, 1903, will also be considered in this section of the paper.

The second section (p. 299) will be concerned with the genera *Serranochromis* Regan 1920 and *Chetia* Trewavas, 1961, together with those '*Haplochromis*' species from the Zambesi, Limpopo and Angola river systems, which were thought to be related to *Serranochromis* and *Chetia* (see Trewavas, 1964).

Section I

HAPLOCHROMIS Hilgendorf, 1888

Type species: *Chromis* (*Haplochromis*) *obliquidens* Hilgendorf, 1888 (type specimens in the Humboldt Museum, Berlin).

Description

Body relatively deep (depth 35–40% of standard length).

Squamation. Scales on the body below the lateral line, and behind a line through the pectoral and pelvic fin insertions, are ctenoid; those above the upper lateral line and on the head and chest are cycloid.

The small scales on the chest grade imperceptibly in size with those on the ventrolateral and ventral aspects of the flanks (p. 270).

Cheek and chest fully scaled.

Lateral line with 29–34 scales (modal range 30–32); all but the last 3 or 4 scales of the upper lateral line are separated from the dorsal fin base by at least two scales of approximately equal size.

Neurocranium. The skull is of a generalized type (see p. 274; Fig. 6, and Greenwood, 1974*a*), its ethmovomerine region having only a slight downward slope, the dorsal surface of the vomer sloping in the same plane and at the same angle as the anterior part of the skull roof; the preotic part of the skull comprises some 55–60% of the total neurocranial length.

Vertebral numbers: 28–30 (modes 28 and 29), comprising 12–14 (mode 13) abdominal and 15 or 16 caudal elements.

Dentition. The outer teeth in both jaws are weakly bicuspid or unicuspid, *the crown of the tooth compressed and noticeably expanded relative to its slender, cylindrical neck and body* (Fig. 7). *The major cusp in bicuspid teeth is very much larger than the minor one, which is often little more than a slight, obliquely truncated basal point on the posterior margin of the anteriorly protracted and slightly incurved* (*i.e. buccally directed*) *major cusp. The compressed, anteriorly protracted and dorsoventrally expanded major cusp gives to the tooth, be it bi- or unicuspid, the appearance of having an obliquely truncated crown. The tip of this cusp lies outside the vertical formed by the anterior margin of the tooth's body.*

All outer teeth, save in some species for a few posterior teeth on the premaxilla, are moveably attached to the underlying bone.

In some species the posterior one to six teeth on the premaxilla are unicuspid or acutely bicuspid, and are stouter and larger than the others in that series; *these posterior teeth in other species of the genus closely resemble, in size and cusp morphology, their anterior congeners.*

Teeth forming the inner rows in both jaws mostly are small and tricuspid, but *in some species the anterior and anterolateral teeth in the outermost row may be identical with those of the outer row.* The inner teeth are arranged so as to form a tooth band that is wide anteriorly and anterolaterally, but narrow posterolaterally. This is effected by an *increase in the tooth rows from the primitive state of two or three to the derived condition of from* 4 *to* 6.

Lower jaw is relatively slender in lateral aspect and not noticeably deepened posteriorly; the length of its dentigerous surface is equal or about equal to the greatest depth of the dentary (as

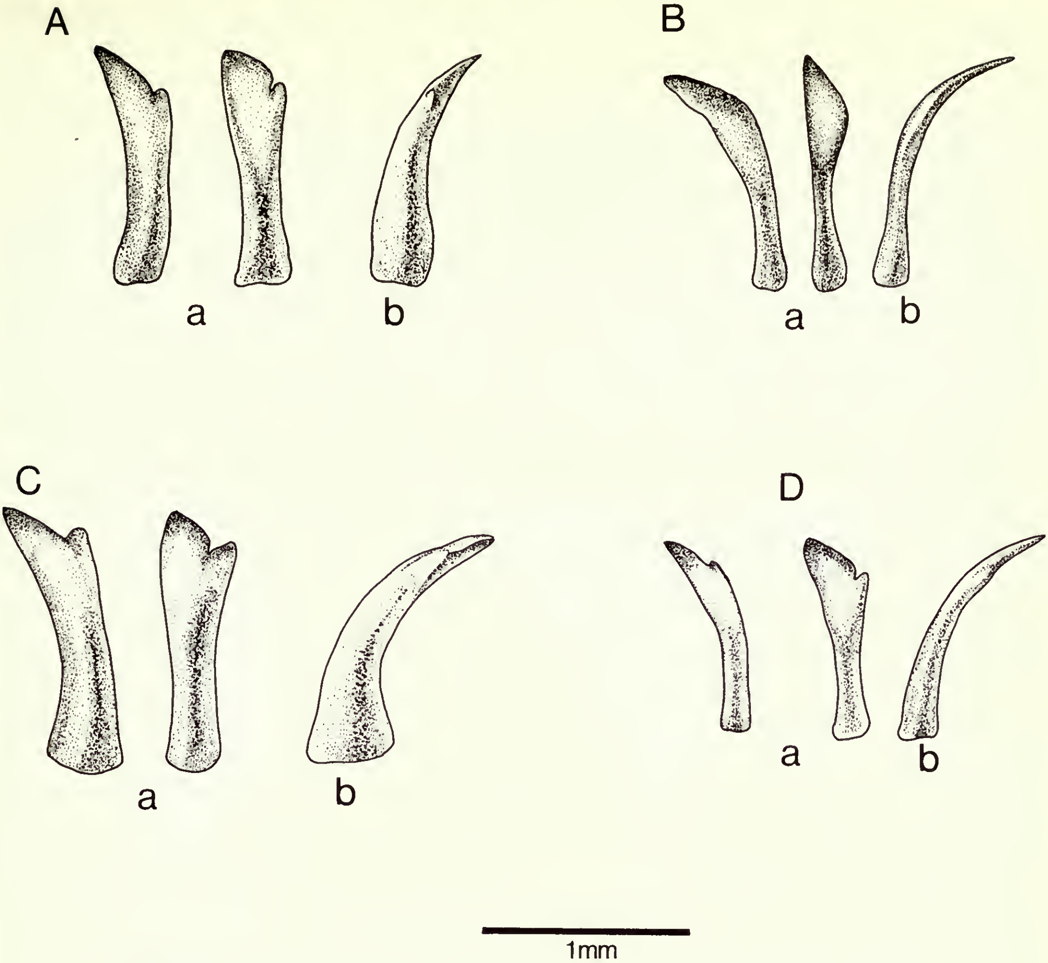

Fig. 7 Outer row jaw teeth (premaxillary) in various *Haplochromis* species; a. labial view, b. lateral (posterior) view. A. *H. annectidens.* B. *H. obliquidens.* C. *H. limax.* D. *H. astatodon.*

measured vertically from the posterior tip of its ascending coronoid process to the ventral margin of the bone).

Lower pharyngeal bone and dentition. The dentigerous surface of the bone is triangular and approximately equilateral in outline (Fig. 8). The teeth, except for those forming the posterior transverse row, are slender with the greater part of the cusp protracted and curved posteriorly so that most of the occlusal surface lies nearly parallel with the surface of the pharyngeal bone. (*The absence of a distinctly coarser median series of teeth probably is a derived feature*; see p. 273.)

Dorsal fin with 14–16 (modes 15 and 16) spinous and 8–10 (mode 9) branched rays.

Anal fin with 3 spinous and 7–10 (mode 9) rays.

Caudal fin skeleton without fusion between any of the hypural elements; none of the species reviewed here was examined by Vandewalle (1973).

Caudal fin truncate or subtruncate, the posterior margin straight or weakly emarginate.

Pelvic fins with the first branched ray the longest.

Anal fin markings. True ocellar egg dummies (see p. 274), *usually* 3 *or* 4 *in a single row, are present in adult males.* Some females may have a similar number of small, non-ocellate spots present in the same position on the fin.

Gill rakers are moderately slender, with 8–10 (mode 9), rarely 7, present on the outer row on the lower part of the first gill arch.

Contained species

Haplochromis obliquidens Hilgendorf, 1888 (Type species). Lake Victoria (see Greenwood, 1956*a*).

Haplochromis lividus Greenwood, 1956. Lake Victoria (see Greenwood, 1956*a*).

Haplochromis annectidens Trewavas, 1933. Lake Nabugabo (see Greenwood, 1965*b*).

Haplochromis limax Trewavas, 1933. Lakes Edward and George (see Greenwood, 1973).

Haplochromis astatodon (part) Regan, 1921. Lake Kivu. When reviewing this species I found that two distinct types of outer jaw dentition are represented amongst the 13 specimens and one skeleton on which Regan (1921*a*) based his original description of the species. That there are two types of teeth represented in this sample is implicit in Regan's comment that the dental morphology of *H. astatodon* is annectant between that of *H. obliquidens* and the simple bicuspid tooth found in many of Lake Victoria '*Haplochromis*' species.

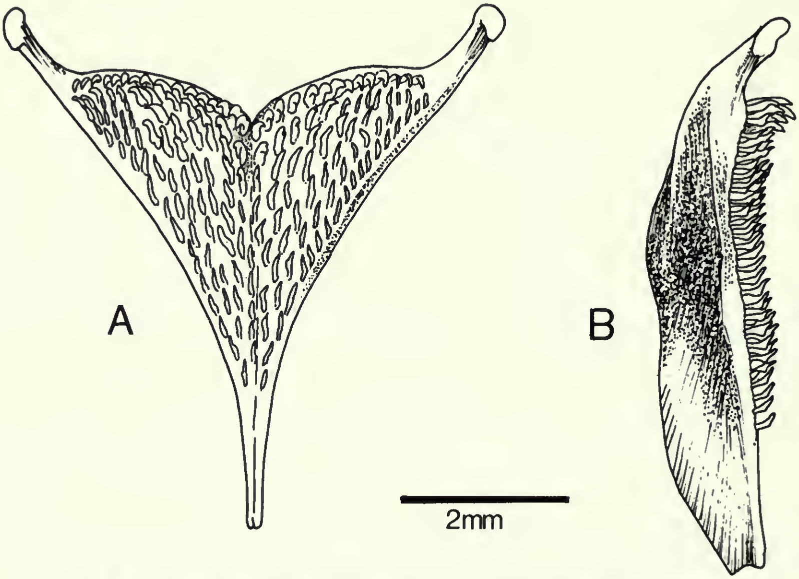

Fig. 8 Lower pharyngeal bone of *H. lividus*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

Six of the syntypical specimens (BMNH reg. nos 1906.9.6 : 124–129) have outer teeth remarkably like those of *H. obliquidens*. That is, the crown is obliquely truncate and greatly produced (Fig. 7D), the neck and body fine, and the teeth are moveably implanted in the gum tissue. However, in these specimens a minute second cusp is present on many of the anterior and anterolateral teeth, a condition seen only amongst some of the posterior teeth in *H. obliquidens*. These particular specimens of *H. astatodon* also resemble *H. obliquidens* in having many teeth in the outermost of the multiseriate inner rows enlarged and often obliquely cuspidate; the inner teeth, like those in *H. obliquidens*, being small and tricuspid.

The pharyngeal dentition in those specimens is also like that in *H. obliquidens*, but the two species differ in certain morphometric features and thus would seem to represent distinct species.

The eight other syntypical specimens of *H. astatodon* (BMNH reg. nos 1906.9.6:130–132; 1977.5.2:1–4 (the material was originally under-registered, hence the lot registered in 1977)), and a skeleton (BMNH reg. no. 1906.9.6:133) have distinctly bicuspid teeth in which the major cusp, although somewhat obliquely truncate, is neither protracted nor expanded, nor is it markedly compressed; the minor cusp is not so greatly reduced as it is in the other syntypical specimens of *H. astatodon*, or in *H. limax*, *H. annectidens* and *H. obliquidens*.

The tooth form and dental arrangement in these aberrant syntypes does, however, approach closely that found in '*Haplochromis*' *nuchisquamulatus* of Lake Victoria and '*H*'. *aeneocolor* of Lake George (see Greenwood, 1956*a* and 1973 for the species respectively).

Because of this marked difference in dental morphology I am restricting the name '*astatodon*' to the six syntypes (BMNH reg. nos 1906.9.6:124–129) with *H. obliquidens*-like teeth, and have selected specimen 1906.9.6:125 as the lectotype. The eight specimens with '*nuchisquamulatus*'-like teeth will be dealt with in a subsequent paper.

Diagnosis and discussion

The lineage here recognized as the genus *Haplochromis* is characterized by having obliquely truncate and protracted crowns to the outer jaw teeth, an increase in the number of rows of inner teeth in both jaws (some of these teeth also having obliquely truncate crowns), and all jaw teeth moveably articulated with the underlying bone. The species are also characterized by their fine lower pharyngeal teeth, and the presence of truly ocellar egg-dummies on the anal fin of adult males. In their gross morphology, and in most aspects of their osteology and anatomy (the greatly elongate intestine excepted), the species retain a generally unspecialized level of organization.

Dental features similar to those of *Haplochromis* do occur in other African Cichlidae, for example *Cyathochromis obliquidens* Trewavas (1935) of Lake Malawi, but are associated with characters which indicate that these other taxa do not share a recent common ancestry with *Haplochromis*. Since all the taxa are grazers on epilithic or epiphytic algae their dental similarities must be considered the results of convergent evolutionary trends.

Within the genus *Haplochromis*, *H. obliquidens* and *H. astatodon* have what appears to be the most specialized (i.e. derived) form of teeth, and *H. limax* the least specialized teeth (see Fig. 7C). The common ancestor could well have been a species with a '*limax*'-like dentition.

In a preliminary phyletic analysis of the Lake Victoria '*Haplochromis*' species flock (Greenwood, 1974*a*), '*H*'. *nigricans* was considered to be the sister species of *H. lividus* and *H. obliquidens*, and '*H*'. *nuchisquamulatus* the sister species of the other three species combined. My recent investigations now suggest, however, that '*H.*' *nigricans* (together with species from Lakes Edward, George and Kivu) form a distinct monophyletic lineage which cannot be related to *Haplochromis* (as here defined) on the basis of shared derived characters. Neither, on those grounds, can '*H.*' *nuchisquamulatus* be considered the sister group of *Haplochromis*. But, it cannot be denied that '*H.*' *nuchisquamulatus* (and at least two other species, including the atypical *H. astatodon* noted above) do have a tooth morphology approaching that of *Haplochromis* (in particular *H. limax*). Tooth form in these species is what might be expected as an early stage of differentiation from the primitive bicuspid type in a morphocline leading to the '*obliquidens*' type. More research is needed before any possible relationship between the five *Haplochromis* species and the '*H.*' *nuchisquamulatus* complex can be clarified.

ASTATOTILAPIA Pellegrin, 1903

TYPE SPECIES: *Labrus desfontainii* Lacépède, 1803 (type specimens, once in the Paris Museum but now apparently lost).

Description

Body relatively deep (35–40% of standard length).

Squamation. Over most of the body the scales are ctenoid, the ctenii generally strong and extending around the greater part of the scale's free margin; scales above the upper lateral line may be less strongly ctenoid than those below it, and in three species are partly or entirely cycloid. Scales on the nape and cheek are cycloid, as may be those on the chest, which is always completely scaled.

The chest scales show a gradual size transition with those on the ventral and ventrolateral aspects of the flanks (see Fig. 1); in some species the chest scales are not noticeably small, but in *A. flaviijosephi*, *A. dolorosa* and *A. desfontainesi* these scales are distinctly smaller (and in *A. calliptera* somewhat smaller) than are the chest scales in other species of the genus.

The cheek is fully scaled, usually with 3 (less commonly 2 or 4) horizontal scale rows.

The lateral line has from 28 to 30 scales (31–33 in *A. desfontainesi*), all but the last 1 to 4 scales of the upper lateral line separated from the dorsal fin base by two or more scales of approximately equal size. *Astatotilapia swynnertoni* is exceptional in having the last 6–8 scales of the upper lateral line separated by less than two scales of equal size.

Neurocranium. The skull is of the generalized haplochromine type (see Greenwood, 1974*a*: 58–59, and p. 274 above). The preotic portion of the skull is not protracted (comprising some 55–60 % of the neurocranial length), and the ethmovomerine region is short, sloping upwards at a slight angle. The dorsal skull roof may be straight or very slightly convex anterodorsal to the orbit. The supraoccipital crest is not reduced in length; its anterior border continues the line formed by the dorsal surface of the ethmovomerine region and the orbital part of the skull roof.

The ventral apophysis for the upper pharyngeal bones (see p. 274) is slightly enlarged in one species (*A. flaviijosephi*). The otic region of the skull is relatively deep, and is not inflated.

Vertebral numbers: 27–30, rarely 26 (modes 28 and 29), comprising 12–14 (mode 13) abdominal and 14–16 (mode 15) caudal elements. The apophysis for the *retractor dorsalis* pharyngeal muscles is small, and situated on the third vertebra.

Dentition. In fishes less than 70 mm standard length unequally bicuspid teeth (Fig. 4) predominate in the outer row of both jaws. The crown in these teeth is not noticeably compressed, neither is it clearly demarcated from the neck of the tooth (cf. *Haplochromis*, p. 278). Except in two species, the cusps are acutely pointed and both lie within the verticals formed by the anterior and posterior margins of the tooth's body; in *A. calliptera* and *A. swynnertoni*, however, at least the major cusp is somewhat obliquely truncate. Unlike *Haplochromis*, the outer teeth in *Astatotilapia* are firmly attached to the bone.

Even in specimens less than 70 mm SL some weakly bicuspid teeth and some unicuspids are found in both jaws. In larger specimens the unicuspid type predominates. The proportion of uni- to bicuspid teeth increases with the size of the individual; *A. dolorosa*, known only from the holotype, a fish 95 mm SL, has only unicuspid teeth.

All species, and specimens of all sizes, have the posterior 3–12 teeth in the premaxilla enlarged and unicuspid.

Teeth forming the inner rows are generally tricuspid and small; some weakly bicuspid or even unicuspid teeth may occur in these rows, particularly in larger fishes. There are 1–3 (usually 2) rows of teeth anteriorly and anterolaterally in both jaws, a single row posteriorly and posterolaterally.

Lower jaw is not foreshortened, nor is it noticeably deepened posteriorly.

Lower pharyngeal bone and dentition. The dentigerous surface is apparently equilateral in all species. Except in *A. flaviijosephi*, all the teeth are compressed, slender and cuspidate, with only those teeth in the two median and the posterior transverse row somewhat coarser than the others. Cusp form is essentially similar to that in *Haplochromis* but the crown is not so markedly produced as in that genus (cf. p. 279 above). In *A. flaviijosephi*, the teeth forming the median rows are enlarged, with molariform or submolariform crowns; some teeth in the lateral rows also are somewhat enlarged and have submolariform crowns. The lower pharyngeal bone, as compared with that in the other species, is stouter.

Dorsal fin with 14–16 (mode 15), rarely 13, spinous rays and 8–11 (modes 9 and 10) branched rays.

Anal fin with 3 spinous and 7–10 (modes 8 and 9) branched rays; specimens of *A. desfontainesi* with 4 spines have been recorded.

Caudal fin skeleton. Astatotilapia burtoni (7 specimens radiographed) and *A. nubila* (9 specimens) show no hypural fusion, but the other 7 species all yielded certain individuals with some degree of fusion in either the upper or the lower set of hypurals, or far less frequently, in both sets. It must be stressed, however, that these observations were made principally from radiographs and that these can be difficult to interpret with accuracy if the hypurals are closely apposed to one another. Vandewalle (1973) reports no fusion in the two specimens of *A. burtoni* he examined. (It is not possible to tell from his paper whether these were radiographed or dissected specimens.)

Caudal fin strongly subtruncate to rounded.

Pelvic fin with the first branched ray longest.

Anal fin markings in male fishes. True ocellar markings are present, usually 2–4 in number (but as many as 9 in large specimens of some species) arranged in one or less commonly in two rows, the number of rows positively correlated with the number of ocelli and the size of the specimen. The row or rows of ocelli run along a line situated approximately midway between the base and the distal margin of the fin. This linear arrangement (and that in *Haplochromis*) contrasts strongly with the near random arrangement of the anal spots in *Serranochromis* and *Chetia* (see pp. 302 and 308 respectively).

No information is available on the occurrence of anal spots (not ocelli, see p. 275) in the females of *Astatotilapia* species, except that 3 or 4 linearly arranged spots do occur in *A. nubila* from Lakes Victoria and George. Trewavas (1973), however, records seeing ripe female *A. nubila* and *A. bloyeti* with male-type ocelli on the anal fin, a phenomenon I never encountered when working with these species in the field.

Where breeding habits are known, *Astatotilapia* species are female mouthbrooders. Indeed, *A. burtoni* is the species on which Wickler (1962*b*) developed his dummy-egg theory to explain the function of anal ocelli in spawning.

Gill rakers of various shapes, from short and stout to moderately long and slender; 8 or 9, less commonly 7, in the outer row on the lower part of the first gill arch.

Contained species

Astatotilapia desfontainesi (Lacép.) 1803 (Type species)*; as restricted by Regan (1922*a*) to specimens from Tunisia and Algeria.

Astatotilapia flaviijosephi (Lortet), 1883. Israel and Syria. See Trewavas (1942) and Werner (1976) for redescription and biology.

Astatotilapia bloyeti (Sauv.), 1883. The type specimens are from Kandoa (Great Ruaha system), Tanzania. Regan (1922*a*) included three other species in the synonymy of *A. bloyeti*, viz. *Ctenochromis strigigena* Pfeffer, 1893, *Tilapia sparsidens* Hilgendorf, 1903 and *Paratilapia kilossana* Steindachner, 1916. For the purposes of this revision I have accepted Regan's synonymy, but much more research is needed into the alpha level taxonomy of fluviatile haplochromine cichlids in eastern and southern Africa before the species can be defined adequately. I have examined material from many localities in Kenya, Uganda and Tanzania, and also from Lake Chad and the Upper Niger. This material would seem to represent a taxon closely similar, if not identical, to *A. bloyeti*, at least on anatomical and morphometric characters. However, judging from colour notes made on certain specimens from Tanzania there are strong indications that at least some populations are distinguishable on the basis of male coloration.

An apparently undescribed species recently distributed by the aquarium trade under the name 'Nigerian mouthbrooder' or 'Nigerian *H. burtoni*' probably should be included in the *A. bloyeti* complex, as should an undescribed species from the Malagarasi river (personal observations).

Until the necessary revision of these 'species' and populations has been carried out, the different taxa involved can be referred to as the '*A. bloyeti* complex' (see Greenwood, 1971). Its distribution includes rivers, streams and certain lakes in Kenya, Uganda, Tanzania, Nigeria and, probably the Nile.

Astatotilapia nubila (Blgr.), 1906. Lakes Victoria, Kioga, Edward, George, Nabugabo, Kachira, Nakavali and Kijanebalola, and river systems in Uganda which are connected with these lakes (see Trewavas, 1933; Greenwood, 1965*b* and 1973). The species has been widely distributed in Uganda (and possibly Kenya and Tanzania as well) as a result of fishfarming and dam stocking activities; its natural distribution is that listed in the first sentence.

Astatotilapia dolorosa (Trewavas), 1933. Known only from the holotype, a specimen collected from the Chambura river which flows into the Kazinga channel connecting Lakes Edward and George.

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* The emended spelling of the trivial name, '*desfontainesi*', was first used by Boulenger (1899). Since Lacépède intended that the species be named for M. Desfontaines, Boulenger's emendation, although not explained, would seem to be justified.

Astatotilapia burtoni (Günther), 1893. Lake Tanganyika and rivers associated with that lake (see Poll, 1956). The specimens recorded from Lake Kivu by Boulenger (1915) were misidentifications (see Regan, 1921*a*).

Astatotilapia stappersi (Poll), 1943. Rivers associated with Lake Tanganyika, see Poll (1956).

Astatotilapia swynnertoni (Blgr.) 1907. Lower Buzi river, Mozambique.

Astatotilapia calliptera (Günther), 1893. Lakes Malawi and Chilwa; '. . . coastal rivers as far as the Save river, Mocambique' (Bell-Cross, 1976); Busi and lower Sabi-Lundi systems; Lower Zambezi and Pungwe systems.

Jubb (1967*a*) treats *A. swynnertoni* as a synonym of this species, but gives no reason for so doing. Judging from the material I have examined, I would consider the two species to be distinct.

Incertae sedis: *Chetia brevis* Jubb, 1968. The presence of 3 or 4 true ocellar markings on the anal fin would seem to exclude this species from the genus *Chetia* (see p. 307 below, and p. 274 above), as would the predominance of ctenoid over cycloid scales on the body, and the retention of bicuspid teeth as the predominant tooth form in specimens as large as 90 mm standard length (see p. 273).

The inclusion of *Chetia brevis* in *Astatotilapia* is, however, very tentative and may well be altered when the phylogeny and systematics of the 'Angolan *Haplochromis*' species are revised (see p. 312).

Diagnosis and discussion

The genus *Astatotilapia* is distinguished from the other fluviatile '*Haplochromis*' group species by the following combination of characters: male anal fin markings are true ocelli, large and usually numbering from 3 to 6, and are arranged in a single or, less frequently, a double row (the number of ocelli and hence the number of rows correlated positively with the size of the fish); scales on the chest region not sharply size-demarcated from those on the ventrolateral and ventral aspects of the body; chest and cheek fully scaled; most body scales are ctenoid, the ctenii on each scale not restricted to a narrow median arc on the scale's free margin but distributed along almost the entire free margin; most teeth in the outer row of both jaws are bicuspid, the cusps of unequal size, but the minor one never minute. The major cusp is acute or, rarely, somewhat obliquely truncate but not protracted (cf. Figs 4 and 7). A few stout unicuspid teeth occur posteriorly in the premaxilla of fishes at all sizes, and some may also be present anteriorly, in both jaws, of fishes > 80 mm SL; the inner teeth usually are tricuspid (occasionally some are weakly bicuspid or unicuspid) and are arranged in two rows anteriorly and anterolaterally; 27–30 (rarely 26) vertebrae, of which 12–14 (mode 13) are abdominal, and 14–16 (mode 15) are caudal elements; pelvic fin with the first branched ray the longest.

Apart from the ocellar anal fin markings, none of these characters can be considered derived, and the anal ocelli are an apomorphic feature shared with *Haplochromis* and most, if not all '*Haplochromis*' species from Lakes Victoria, Edward, George and Kivu, and some species from Lake Malawi as well. Thus, the possibility cannot be overruled that *Astatotilapia* is a non-monophyletic assemblage.

The absence of other synapomorphic features shared with the genera described in this paper at least indicates that no members of *Astatotilapia* are closely related to any one of those lineages (as was implied when, hitherto, most were placed in the genus *Haplochromis*).

The relationship of *Astatotilapia* to *Haplochromis* as now redefined is obscure. Both lineages share the apomorphic feature of anal ocelli, suggesting that both share a more recent common ancestry than either lineage does with any taxa not having this feature. Uncertainty also exists about the relationship between *Astatotilapia* and the anal ocelli-bearing lineages of Lakes Victoria, Edward, George and Kivu, and for that matter some of the anatomically generalized '*Haplochromis*' species of Lake Malawi.

Any member of the *Astatotilapia* line with acutely bicuspid teeth (except, because of its specialized pharyngeal mill, *A. flaviijosephi*) could, on purely morphological grounds, be taken to represent the ancestral species for many lineages within the Victoria–Edward–Kivu species flock (see Greenwood, 1974*a*). It is, indeed, likely that a number of generalized but endemic species from that flock will have to be included in *Astatotilapia*, as may some from Lake Malawi.

Relationships within the *Astatotilapia* lineage cannot be indicated at present, partly because no intragroup synapomorphies are apparent and partly because the species are as yet poorly defined and understood (see p. 283).

Astatotliapia, like *Thoracochromis* (see p. 290) has a wide geographical distribution (one, indeed that extends beyond Africa into the Middle East). Both genera occur in north Africa, although *Astatotilapia* does not apparently occur in the Nile drainage (except in Lakes Victoria and Kioga); *Thoracochromis*, on the other hand, is widely distributed in the Nile system but is poorly represented, if at all, in Lake Victoria, and does not extend so far into southern Africa as does *Astatotilapia*.

In general, it could be said that *Astatotilapia* is a lineage of eastern and southern Africa, with outliers in the northeast (*A. flaviijosephi*) and northwest (Algeria and Tunisia), and *Thoracochromis* a lineage of north, central and western Africa. Since the phyletic integrity of both lineages is uncertain (see above, and p. 294), and because large parts of the Zaire system are poorly known, this difference may be more artefactual than real.

ASTATOREOCHROMIS Pellegrin, 1903

TYPE SPECIES: *Astatoreochromis alluaudi* Pellegrin, 1903 (type specimens in the Paris Musuem). For synonymy see Greenwood (1959*a*) and discussion below.

Discussion

Pellegrin (1903) distinguished *Astatoreochromis* (then monotypic) from similar '*Haplochromis*'-group species and genera principally on its having 5 or 6 anal and 18 or 19 dorsal fin spines. The type species is from Lake Victoria, but later, specimens were collected from Lakes Edward and George, the Victoria Nile and Lakes Kioga, Nakavali and Kachira (see Greenwood, 1959*a*).

Redescriptions based on this enhanced material added to the number of diagnostic features, at least with respect to the '*Haplochromis*' species of Lakes Edward and Victoria (Greenwood, 1959*a*). Amongst those features are the rounded caudal fin, the high number and multiserial arrangement (3 or 4 rows) of the anal ocelli in male fishes, the unusual coloration (golden overlain with olivaceous green, the median fins olive-yellow, flushed with maroon and margined with black), and the lack of sexual dimorphism in basic body and fin colours. This material also extended the known range of dorsal fin spine numbers (16–20) as well as those of the anal fin (4–6).

The species *Astatoreochromis alluaudi* is further characterized by its strongly hypertrophied crushing pharyngeal dentition and bones (with a correlated hypertrophy of the cranial apophysis for the upper pharyngeal bones; see Greenwood, 1959*a* and 1965*a*). A similar degree of pharyngeal hypertrophy does, of course, occur in at least five other species from Lakes Victoria, Edward and George (Greenwood, 1960 : 270–279; 1973 : 172–177; Greenwood & Barel, 1978 : 164–179), but these species differ from *A. alluaudi* in several features, all of which suggest that *A. alluaudi* represents a distinct phyletic lineage.

The principal diagnostic characters for *Astatoreochromis* are not easily assessed on a basis of their apo- or plesiomorphy. The enlarged pharyngeal mill clearly is a derived feature, but is one that has evolved independently in at least two '*Haplochromis*' lineages (see Greenwood, 1974*a*, and p. 279 above); it is thus of little value in assessing relationships at the level with which we are here concerned.

As yet too little is known about the evolution and phyletic distribution of anal ocelli (and other anal fin markings) to say whether the increased number and multiserial arrangement in *Astatoreochromis* is a derived feature. The basis for comparison here is with the fewer ocelli and their uni- or biserial arrangement in *Haplochromis*, *Astatotilapia* and the Lake Victoria '*Haplochromis*' species.

The absence of sexually dimorphic coloration in *Astatoreochromis* is a most unusual feature amongst '*Haplochromis*'-like taxa, but would seem, *a priori*, to be a primitive rather than a derived feature (although its correlation with the increased number of anal ocelli and thus, possibly its degree of relative importance in breeding behaviour, cannot be interpreted without appropriate ethological studies).

Only the increased number of anal and dorsal fin spines (*but, it should be noted, not the total number of rays in these fins*) *would seem to be derived features.*

In the absence of other and synapomorphic characters, however, it is impossible to use fin spines numbers to suggest any possible close phyletic affinities for *Astatoreochromis*. For example, the squamation pattern in the genus is of the supposedly plesiomorph type, and this would seem to rule out any possible relationship with the *Orthochromis* lineage (see p. 295) in which there is also a marked trend towards increased numbers of dorsal and anal fin spines. *Orthochromis*, it may be added, does not have anal ocelli or, apparently, any other anal fin markings in the males (the breeding habits of no *Orthochromis* species are recorded).

That *Astatoreochromis* may be related (possibly as the derived sister-group) to some of the '*Haplochromis*' species with enlarged pharyngeal mills, cannot be completely discounted; but, equally there is little unequivocal evidence to support such an hypothesis (see above).

For the moment, then, *Astatoreochromis* is maintained as a distinct lineage because of its various distinctive features, taken in combination, and because its sister-group relationship to any other lineage cannot be hypothesised on the basis of uniquely shared derived characters.

Recently, Poll (1974) added a second species (*Haplochromis straeleni* Poll, 1944, from the Lukuga and Ruzizi rivers, Zaire) to the genus *Astatoreochromis*. This step was taken because some specimens of *straeleni* have 4 anal spines (i.e. 2 of the 7 specimens known), because of close similarities in overall coloration and in the pattern and number of anal ocelli, and because *straeleni* has a relatively enlarged lower pharyngeal bone with some molariform teeth (see fig. 1, Poll, 1974). The species also has, as compared with *Astatotilapia* and the Lake Victoria '*Haplochromis*' species, more dorsal fin spines (17 or 18) but the same number of branched rays in that fin (8 or 9); in other words, the *Astatoreochromis* condition (see above). Furthermore, according to Poll's account, there is no sexually dimorphic coloration in '*H.*' *straeleni*.

There is another '*Haplochromis*' species, '*H*'. *vanderhorsti* Greenwood, 1954 (Malagarasi river, Tanzania) which closely resembles *straeleni* in all the characters under consideration, differing only in its slightly lower dorsal fin spine count (16 or 17), and in none of the 54 specimens examined having 4 anal fin spines; its lower pharyngeal bone and dentition are more massive than those of *straeleni* (i.e. like the condition in *A. alluaudi* of the same size). The resemblances between '*H.*' *vanderhorsti* and *A. alluaudi*, and those between '*H.*' *straeleni* and '*H.*' *vanderhorsti* have been noted already (Greenwood, 1954 : 405–407; 1959*a* : 166–167), but were not analysed in terms of their apo- or plesiomorphy, and no conclusion was reached about the interrelationships of the species or their formal taxonomic status.

Apart from the increased number of dorsal fin spines (and the four-spined individuals of '*H.*' *straeleni*), the only other shared, and probably derived, characteristic common to the three species is the enlarged lower pharyngeal bone and its at least partly molariform teeth (again a trend character, least developed in *straeleni*, most developed in *Astatoreochromis alluaudi*, and one which is known to have evolved independently in several haplochromine lineages). But, taking into account the virtually identical, non-sexually dichromatic coloration of the three species (and the ubiquity of sexual dichromatism alongst fluviatile haplochromines) the most parsimonious solution would be to consider *alluaudi*, *straeleni* and *vanderhorsti* as being more closely related to one another than any one of them is to any other lineage.

On these grounds I would agree with Poll's (1974) inclusion of '*H.*' *straeleni* in *Astatoreochromis* and would now include '*H.*' *vanderhorsti* in that genus as well.

Contained species

Astatoreochromis alluaudi Pellegrin, 1903 (Type species). Lakes Victoria, Kioga, Edward, George, Nabugabo, Kachira, and Nakavali; rivers and streams associated with these lakes. The species has been widely distributed in Kenya, Uganda and Tanzania as a biological control agent against snails (McMahon, Highton & Marshall, 1977). For a full description of the species see Greenwood (1959*a*), and for evidence invalidating the two subspecies described in that paper see Greenwood (1965*a*).

Astatoreochromis straeleni (Poll), 1944. Lukuga and Ruzizi rivers, Lake Tanganyika drainage. See Poll (1974) for a redescription of the species.

Astatoreochromis vanderhorsti (Greenwood) 1954. Malagarasi river and swamps, Lake Tanganyika drainage.

CTENOCHROMIS Pfeffer, 1893

TYPE SPECIES: *Ctenochromis pectoralis* Pfeffer, 1893 (type specimens in Hamburg Museum and BMNH).

Description

Body relatively deep to relatively slender (depth 30–40% of standard length).

Squamation. Scales on the body below the upper lateral line are strongly to moderately ctenoid (weakly ctenoid in one species, *C. horii*), becoming cycloid over the posterior half of the body. Scales above the upper lateral line show the same range of ctenoidy or are all cycloid, the kind of scale being constant intraspecifically and positively correlated with those below the lateral line. Scales on the head and, when present, on the cheek, are cycloid.

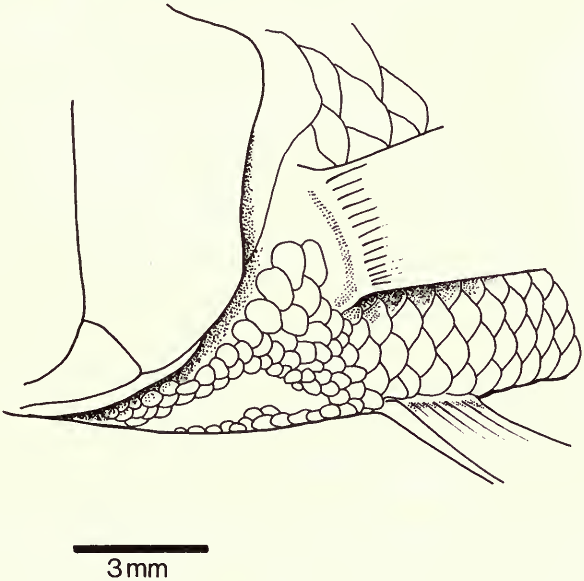

Fig. 9 Thoracic–abdominal scale transition in *Ctenochromis pectoralis*. Left lateral view.

The cheek always has a naked area along its ventral margin; in one species this area is less than a scale row in depth, in two others it is from 1 *to* 3 *horizontal scale rows deep, and in a fourth virtually the whole cheek is naked, a few scales remaining immediately below and, or, behind the orbit.*

Along or slightly behind a line joining the pectoral and pelvic fin bases there is an abrupt size transition between the very small scales on the chest and the much larger scales on the lateral and ventrolateral aspects of the body (Fig. 9).

The chest has a well circumscribed naked patch on each side of the body (Fig. 9), *the two patches joined in some species by a ventral naked area.* The size of the naked patch shows some interspecific variability, from a small and ventrolaterally situated area, to one covering most of the lateral and ventrolateral (but not the medial) aspects of the chest.

There are 27–33 scales in the lateral line series (modal numbers 30 and 31 for the two species from Tanzania, and 28–30 for the three Zaire river system species (see p. 290 below)); *the last* 8–12 (*usually* 8 *or* 9) *pored scales in the upper lateral line are separated from the dorsal fin base by less than two scales of approximately equal size.*

Neurocranium. The neurocranium is apparently of the generalized type (see Fig. 6), but in at least one species (*C. horii*; Fig. 10) its preotic region is more elongate (*c.* 68–70% of neurocranial length) and in others the preorbital region is slightly vaulted. Since little skeletal material is available these remarks are based mainly on radiographs and should be checked on actual skeletons.

Vertebral numbers: 25–29 (modal range 27–28), comprising 12 or 13 abdominal and 13–17 caudal elements (see p. 290 below).

Dentition. The outer teeth are unequally bicuspid, or, in two species, subequally bicuspid, are relatively stout and firmly attached to the underlying bone. Some posterior premaxillary teeth (as many as 16 on each side in *C. horii*) are unicuspid, caniniform and relatively larger than the preceding bicuspids. The crowns of the bicuspid teeth are not noticeably compressed, nor are they sharply demarcated from the shaft of the tooth; the cusps are acutely pointed.

The inner teeth are small and tricuspid, and arranged in 2 or 3 series anteriorly and anterolaterally, but a single series posteriorly.

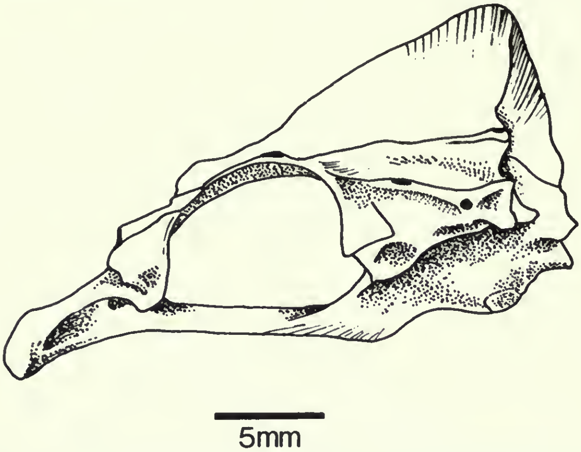

Fig. 10 Neurocranium of *Ctenochromis horii*; left lateral view.

Lower jaw. The dentary is relatively slender in lateral aspect, and not greatly deepened posteriorly.

Lower pharyngeal bone and teeth. The dentigerous surface is either triangular and subequilateral (slightly broader than long) in outline, or noticeably broader than long (*c*. 1½ times; Fig. 11). The teeth are cuspidate and compressed, those in the median and the posterior transverse row somewhat stouter than the others (the degree of stoutness, especially of teeth in the two median rows, shows a positive correlation with the fish's size).

Dorsal fin with 14–17 (modes 15 and 16) spinous and 8–10 (mode 9) branched rays. The holotype of *C. oligacanthus* (Regan) has only 12 spines, but all other specimens have 15.

Caudal fin skeleton. Because few dry skeletons or alizarin preparations are available, information on the caudal skeleton has been obtained mainly from radiographs. The difficulty of differentiating between fused and closely apposed hypural elements as seen in radiographs makes these observations of limited value.

Ctenochromis pectoralis (10 specimens radiographed) has all five hypurals free.

C. horii. Seven specimens (radiographed) have hypurals 1 and 2, and 3 and 4 fused, as does the dry skeleton examined. Two other specimens (radiographed) have hypurals 1 and 2 free, but 3 and 4 fused. Vandewalle (1973) found no fused hypurals in the two specimens he examined.

C. polli (2 specimens radiographed) has all hypurals free.

C. oligacanthus. Of the three specimens radiographed, one (the holotype) has all hypurals free, one has hypurals 1 and 2 free but 3 and 4 fused, and the third has hypurals 1 and 2, and 3 and 4 fused.

Caudal fin is markedly subtruncate, almost rounded in some species.

Pelvic fin with the first branched ray the longest.

Anal fin markings in male fishes. Where known (3 of the 5 species) from preserved and, or, living specimens, these are in the form of one or two (rarely three) brilliant white or yellow spots, without a dark margin and without a clear surround (cf. *Haplochromis* and *Astatotilapia*, p. 279 and

p. 283 respectively). The spot or spots may be on the anterior or the posterior part of the soft fin with, apparently, their position constant intraspecifically. For a colour picture of *C. polli* see Voss (1977 : 74).

Gill rakers short and stout in all species except *C. horii* where they are long and slender; there are 7–9 rakers in the outer row on the first gill arch, except in *C. horii* where there are 10–13.

Contained species

Ctenochromis pectoralis Pfeffer, 1893 (Type species). Known only from streams in south eastern Tanzania, near Korogwe.

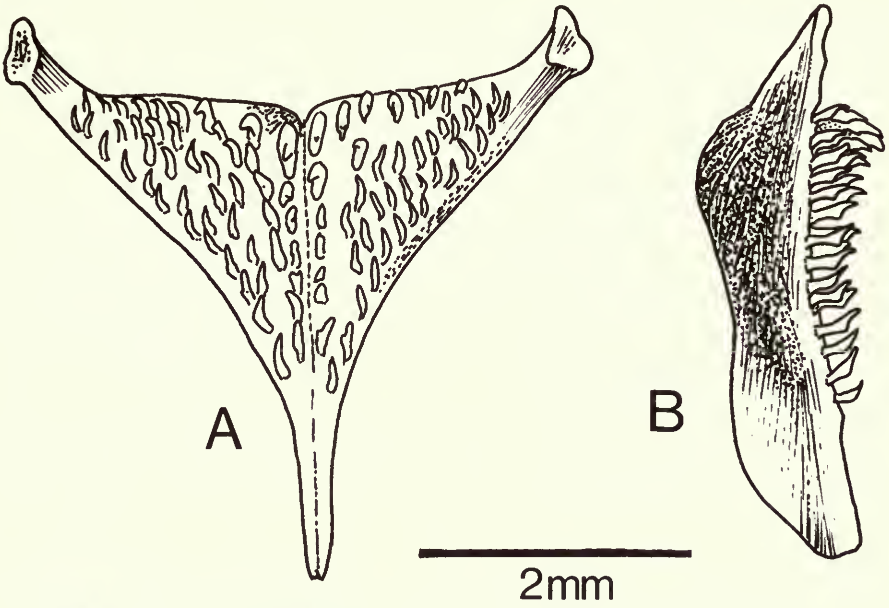

Fig. 11 Lower pharyngeal bone of *Ctenochromis polli*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

Ctenochromis horii (Günther), 1893. Lake Tanganyika and the coastal reaches of associated rivers. See Poll (1956) for a detailed description and notes on biology.

Ctenochromis polli (Thys van den Audenaerde), 1964. Pool Molebo (Stanley Pool) and the lower Zaire river. For coloured plate see Voss (1977). For notes regarding specimens formerly identified as *H. fasciatus* see p. 293.

Ctenochromis oligacanthus (Regan) 1922. Ubangi river, an affluent of the Zaire river. The holotype and sole specimen available to Regan has only 12 dorsal fin spines and 9 branched rays; the two additional specimens I have examined have 15 spines and 9 branched rays.

Ctenochromis luluae (Fowler), 1931. Lulua river, Kasai drainage system, lower Zaire. I have examined four paratypes, and on the basis of that material would consider the species to be distinct from *C. polli* and *C. oligacanthus* (the other two *Ctenochromis* from the lower Zaire drainage), and from *C. pectoralis* and *C. horii*.

Diagnosis and discussion

Members of the genus *Ctenochromis* are characterized by the abrupt size transition between the very small chest scales and the larger scales on the ventrolateral aspects of the anterior flanks, by a naked area on either side of the chest, and by a failure of the cheek squamation to reach the ventral margin of the cheek. (In one species, *C. horii*, the entire suborbital region of the cheek is scaleless in some individuals and in others there is, at most, no more than a single scale row below and behind the orbit.) In three of the five species the anal fin markings of male fishes are in the form of one or two (rarely three), relatively small and simple, non-ocellate spots; no information is available on the other two species.

Virtually nothing is known about the biology of *Ctenochromis* species, which are, with the exception of *C. horii*, very poorly represented in study collections. Four of the five species are fluviatile and reach a small adult size (80 mm standard length); their feeding and breeding habits are unknown. The fifth species, *C. horii*, is essentially lacustrine, reaches a larger adult size (185 mm SL) and is at least partly piscivorous.

The geographical range of *Ctenochromis* extends from Tanzania in the east to the Zaire drainage (including Lake Tanganyika) in the west and lies between the latitudinal limits of *c.* 3° N and 8° S.

Various apomorph features shown by *Ctenochromis* suggest its relationships with two other genera; this problem will be discussed later (see p. 313).

Intrageneric relationships are difficult to determine, partly because the small size of some specimens limited the amount of anatomical information that could be obtained, partly because of the mosaic interspecific distribution of certain presumed apomorph characters, and partly because other characters form part of a morphoclinal continuum.

Both *C. pectoralis* (eastern Tanzania) and *C. horii* (Lake Tanganyika) have, relative to *C. polli* and *C. oligacanthus*, higher caudal vertebral counts (15–17, modes 16 and 17, cf. 13 and 14) and higher lateral line scale counts (29–33, modes 30 and 31, cf. 27–29, mode 28); these features should probably be considered plesiomorph ones (see p.276). *Ctenochromis pectoralis* has relatively small naked patches on the chest (Fig. 9), and only the lower part of the cheek is scaleless. In comparison, *C. horii* has a large naked area on the chest and almost the entire cheek is without scales; the neurocranium in this species departs somewhat from the basic type found in *C. pectoralis* (see Fig. 10 and p. 287) in having larger preorbital and preotic proportions, and individuals reach a larger size than in *C. pectoralis*. On these grounds I would consider *C. horii* to be the derived sister species of *C. pectoralis*.

Ctenochromis polli (Stanley Pool and the lower Zaire river) and *C. oligacanthus* (Ubangi river, Zaire drainage) both have a reduced number of caudal vertebrae (13 or 14), fewer lateral line scales (27–29) and fewer branched anal fin rays (6 or 7 cf. 8 or 9 in *C. pectoralis*; *C. horii* with 7 (mode) or 8 anal rays occupies an intermediate position).

The third lower Zaire species, *Ctenochromis luluae* (Lulua river), however, also has an intermediate number of anal fin rays (7 or 8, mode 8), of lateral line scales (28–30) and of caudal vertebrae (15).

The outer jaw teeth in *C. polli*, *C. luluae* and *C. oligacanthus* are similar and differ from the basic, unequally bicuspid type found in *C. horii* and *C. pectoralis* in having the cusps subequal in size, with the tip of the smaller cusp directed away from the near vertical larger cusp. In both *C. polli* and *C. oligacanthus* the dentigerous surface of the lower pharyngeal bone is noticeably broader than long, whereas in *C. pectoralis* and *C. horii* its length and breadth are approximately equal (see Fig. 11); the bone in *C. luluae* has proportions that are intermediate between these two types. Finally, the naked area of the chest in *C. oligacanthus* is much larger than in *C. polli*, but a greater area of the cheek is scaled in the former species. Most of the cheek is scaled in *C. luluae*, and the naked chest area is intermediate between that of *C. polli* and *C. oligacanthus*.

On the basis of their dental morphology I would suggest that *C. polli*, *C. luluae* and *C. oligacanthus* together form the sister group to *C. pectoralis* and *C. horii*; *C. pectoralis* would seem to be the least derived taxon of the lineage.

As a postscript to this discussion it may be mentioned (with the reservations noted on p. 282) that hypural fusions in *Ctenochromis* species are relatively common, and certainly commoner than in *Haplochromis*, *Astatotilapia* and the '*Haplochromis*' species of Lake Victoria (see p. 276 above, and Greenwood, 1974*b* : 159).

THORACOCHROMIS gen. nov.

TYPE SPECIES: *Paratilapia wingatii* Boulenger, 1902 (see Greenwood, 1971 for a redescription of the species).

ETYMOLOGY. The name is derived from the latinized Greek word for a breastplate + *chromis*, a name when used in such a combination now associated with many genera of African Cichlidae;

it refers to the small and clearly size-demarcated scales on the thoracic region of species in this lineage.

Description

Body form ranging from relatively deep to relatively slender (depth 30–40% of standard length).

Squamation. In the majority of species, the scales on the body above and below the upper lateral line, and behind a line through the pectoral and pelvic fin insertions, are ctenoid. A few species have cycloid scales above the upper lateral line, and weakly ctenoid scales below it. Scales on the cheek, head and chest are cycloid.

The scales on the chest are small to very small and meet, with an abrupt change in size, the larger scales on the lateral and ventrolateral aspects of the flanks (Fig. 2). Generally the line of this abrupt size change lies approximately between the insertions of the pectoral and pelvic fins, but may be a little behind or, less frequently, a little before that level. The chest is always completely scaled, although in two species the scales are so small and deeply embedded that the area appears to be naked.

The cheek is completely or almost completely scaled (in two species there is a very narrow, horizontal naked strip along the ventral margin, and in several other species there is a naked embayment at the anteroventral angle of the cheek squamation).

There are 29–32 (modal range 30–32) scales in the lateral line series; *about the last eight pore-bearing scales of the upper lateral line are separated from the dorsal fin base by not more than one large and one much smaller scale.*

Neurocranium. Most *Thoracochromis* species have a skull form that departs but slightly from the type found in *Ctenochromis* (see p. 287). That is, a generalized type (see p. 274) in which the preotic region of the neurocranium comprises some 65–70% of the total neurocranial length.

The most marked departure from this skull form is seen in two species, *Th. bullatus* (Lake Albert) which has a greatly inflated otic capsule and somewhat enlarged lateral line sensory canals, and *Th. macconneli* (Lake Turkana) where the sensory canals are hypertrophied and the braincase is shallower.

Thoracochromis demeusii (Zaire) deviates in a different way; here the supraoccipital crest is deepened, extends further anteriorly than in the other species and has a steeper slope to its anterior margin. These features may all be associated with the pronounced dermal hump developed in the nuchal region of this species.

Vertebral numbers: 26–31 (modes 28 and 29), comprising 12–14 (modes 12 and 13) abdominal and 13–17 (modes 14 and 17) caudal elements. With one exception (*Th. moeruensis*) the lower modal counts for caudal vertebrae are found in fluviatile species from the Zaire river drainage system, the higher ones in species from Lakes Turkana, Albert, George and Mweru.

Dentition. Unequally bicuspid or unicuspid, caniniform outer teeth are the the most frequently occurring types. The crown in bicuspids is not noticeably compressed, and the cusps are acutely pointed. Unicuspid teeth may be recurved or almost straight; where the material covers a sufficiently wide size range of specimens it shows that the unicuspid dentition is preceded by a bicuspid one. Fishes in all species with a bicuspid definitive dentition have a few (1–6) unicuspids posteriorly on the premaxilla, these teeth generally being larger than the anterior bicuspids.

In two species (*Th. fasciatus* and *Th. loati*) the outer teeth, although unequally bicuspid, have the major cusp obliquely truncate, somewhat protracted and relatively compressed; the minor cusp is much reduced and is also obliquely truncate. Thus there is a close resemblance between these teeth and those in *Haplochromis lividus* and *H. limax* (see Fig. 7C and p. 281 above; also Greenwood, 1971 : 360, fig. 5).

The inner teeth generally are tricuspid and in both jaws are arranged in 2 or 3 series anteriorly and laterally, but in a single series posteriorly. In those species with unicuspid outer teeth at least the outermost row of the inner series contains some unicuspids, a mixture of tri- and unicuspids, or it may be composed entirely of unicuspids.

Lower jaw relatively slender in lateral outline and not obviously deepened posteriorly.

Lower pharyngeal bone and teeth. With respect to the outline shape of the dentigerous area, two fairly distinct types of pharyngeal bone occur in this genus. One type (found in species of the Zaire drainage, including *Th. moeruensis* but excluding *Th. demeusii*) has the surface clearly broader than long (Fig. 12). The second type (in species from Lakes Turkana, Albert and George) has its dentigerous surface only slightly broader than long, i.e. about 1⅕ times.

In all species the median tooth rows are noticeably coarser than their lateral congeners, and are even coarser than those in the posterior transverse row. Some species have stout and molariform or submolariform teeth in the median rows, and in three other species (*Th. albertianus*, *Th. mahagiensis* and *Th. pharyngalis*) teeth lateral to the median rows are also enlarged and submolariform to molariform, (see Trewavas, 1938 : 441 and 444; Poll, 1939 : 47; Greenwood, 1973 : 213). Associated with this enlargement of the dentition (especially in *Th. mahagiensis* and *Th. pharyngalis*) the lower pharyngeal bone is markedly thickened.

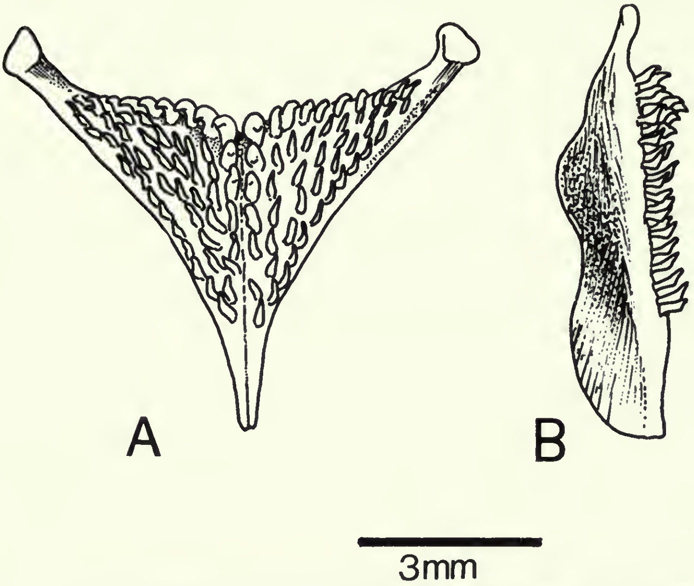

Fig. 12 Lower pharyngeal bone of *Thoracochromis bakongo*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

Teeth other than the enlarged ones are compressed and cuspidate in all species.

Dorsal fin with 13–16 (modal range 14–16), rarely 17, spinous and 8–10 (modes 9 and 10), rarely 11, branched rays.

Anal fin with 3 spines and 6–10 (modal range 7–9) branched rays.

Caudal fin skeleton: the distribution of fused hypural elements amongst *Thoracochromis* species, as determined mainly from radiographs, is as follows:

(i) Lake Albert species, and those from the Nile and Lake George: no fusion in *Th. wingatii* (holotype), *Th. albertianus* (6 specimens), *Th. mahagiensis* (1), *Th. avium* (holotype), *Th. bullatus* (13), *Th. loati* (16) and *Th. petronius* (12); some specimens in most species have certain hypurals very closely apposed.

(ii) Lake Turkana. *Th. rudolfianus* has all hypurals free in 28 specimens examined, but hypurals 1 and 2 are closely apposed or perhaps fused in two others; *Th. turkanae* (4 specimens) has all hypurals free; in *Th. macconneli* 6 of the 26 specimens examined have all hypurals free, 4 have hypurals 1 and 2, and 4 and 5 fused, 11 have hypurals 1 and 2, and 3 and 4 fused, but hypural 5 free, and 5 have only hypurals 1 and 2 fused.

(iii) Lower Zaire drainage, and Lake Mweru. *Th. moeruensis* has hypurals 1 and 2, and 3 and 4 fused (6 specimens). *Th. demeusii* (holotype) has all free; *Th. fasciatis* (6 syntypes) has all free, as does *Th. bakongo* (3 specimens); *Th. stigmatogenys* has 2 specimens with hypurals 3 and 4 fused, and 4 others with all hypurals free. Vandewalle (1973) reports no fusion in the two species he examined, namely, *Th. bakongo* and *Th. fasciatus*.

Caudal fin subtruncate to almost rounded, most species being in the latter category.

Pelvic fin with the first branched ray the longest.

Anal fin markings. Regrettably little information is available on this character, either from live or preserved specimens. True ocellar spots (3–8 in number) are present in *Th. petronius* (Lake George) and apparently in the three species from Lake Turkana, although the clear surround in these latter species is much narrower than in the ocelli of *Haplochromis* and *Astatotilapia*. The four species from Lake Albert and the Nile for which data are available (i.e. *Th. albertianus*, *Th. bullatus*, *Th. wingatii* and *Th. loati*) do not appear to have any clear area around the small, coloured or white spots, which are relatively large, well defined and number from 1 to 3. However, these observations were made on preserved material only and, since the whole fin is somewhat pigmented, a narrow hyaline surround could well be overlooked.

No information is available for the remaining species (Lake Mweru and the Zaire river drainage).

Gill rakers are of various shapes, with 6–12 (modal range 7–9) in the outer row on the first gill arch.

Contained species

Thoracochromis wingatii (Blgr.), 1902, type species; see Greenwood (1971) for a redescription and definition of the species. Upper Nile (Bahr-el-Jebel) and probably Lake Albert also.

Thoracochromis loati (Greenwood), 1971. Upper Nile (Bahr-el-Jebel) and Lake Albert.

Thoracochromis rudolfianus (Trewavas), 1933. Lake Turkana.

Thoracochromis turkanae (Greenwood), 1974. Lake Turkana.

Thoracochromis macconneli (Greenwood), 1974. Lake Turkana.

See Greenwood (1974*b*) for notes on the biology of the last three species, and for comments on their relationships.

Thoracochromis albertianus (Regan), 1929. Lake Albert.

Thoracochromis mahagiensis (David & Poll), 1937. Lake Albert (see also Greenwood, 1971 : 356).

Thoracochromis avium (Regan), 1929. Lake Albert. I follow Trewavas (1938) in considering *Haplochromis lanceolatus* David & Poll, 1937, a synonym of this species.

Thoracochromis petronius (Greenwood), 1973. Lake George, Uganda.

Thoracochromis pharyngalis (Poll), 1939. Lake Edward. See Greenwood (1973 : 213) for a discussion on the relationship of this species.

Thoracochromis moeruensis (Blgr.), 1899. Lake Mweru.

Thoracochromis demeusii (Blgr.), 1899. Lower Zaire river. See Thys van den Audenaerde (1964) for a redescription of the species and for other data; this author considers that the presumed type locality (Bangala country, Upper Congo) is in error.

Thoracochromis bakongo (Thys van den Audenaerde), 1964. Kasai drainage to the lower Zaire river.

Thoracochromis fasciatus (Perugia), 1892. Lower Zaire drainage at Vivi (5°38′ S, 13°30′ E; see Thys van den Audenaerde, 1964). At present I am restricting the concept of this species to the six syntypical specimens in the BMNH collections (reg. nos 1898.12.12:1–6). Certain other specimens in the BMNH collections identified as *fasciatus*, and at least part of the material on which Thys van den Audenaerde (1964) based his redescription of the species, are referable to one or possibly two other species. These, or this, species differ from the syntypes of *fasciatus* in dental characters and in having a graded rather than an abrupt size change between the chest and ventrolateral flank scales (i.e. they cannot be referred to the genus *Thoracochromis*; see p. 291 above).

Three further specimens in the BMNH collections (reg. nos 1899.9.6:2–4, ex Stanley Pool) which were included in *fasciatus* by Boulenger (1915 : 215–216) do, however, show an abrupt size change in the scales of this region. All 3 specimens are now in a very poor state of preservation but, judging from certain morphometric characters and also from their dental morphology, it seems that they should be identified as *Ctenochromis polli* (see p. 289).

Regan (1922*a*) tentatively included *Paratilapia toddi* Blgr., 1905 (Kasai river, Zaire drainage) in the synonymy of *fasciatus*. Regan's concept of *fasciatus* was essentially that of Boulenger (1915) since his study material included the misidentified specimens noted above. The only known specimen of *Paratilapia toddi*, the holotype, is considerably larger (127·0 mm SL) than any member of a known *Thoracochromis* species, and has the general facies and external cranial morphology of a *Serranochromis*-like fish (see Trewavas (1964) who, indeed, thought that *P. toddi* might be related to *Serranochromis*). However, the holotype of *P. toddi* does show an abrupt size transition between the scales of the chest and flanks, and it also has a low number of caudal vertebrae (13) and a low branched anal fin ray count (7), features shared with some species of *Thoracochromis* (see p. 291 above). On the other hand, there are several features of *P. toddi* that are not encountered in any member of that genus.

Until more specimens are available it would seem best to treat *P. toddi* as a taxon *incertae sedis*; it certainly cannot be considered a synonym of *Thoracochromis fasciatus*.

Thys van den Audenaerde (1964) considers Boulenger's (1899) *Chromis monteiri* (from Boma) to be a synonym of *fasciatus*. Regrettably the holotype (and unique) specimen of *C. monteiri* cannot now be found and so a comparison between it and the syntypes of *Th. fasciatus* could not be made. But, judging from Boulenger's original description and figure, it seems highly improbable that the specimens are from the same species. The possibility that *monteiri* holotype and some of the misidentified *fasciatus* material are conspecific cannot, however, be overlooked.

Diagnosis and discussion

Members of the genus *Thoracochromis* are characterized by the abrupt size transition between the small chest scales and the much larger scales on the ventrolateral and ventral aspects of the flanks. This is, apparently, the only derived character shared by all members of the lineage. Several other derived features are, however, found in member species. For example, the obliquely truncate tooth cusps in *Th. loati* and *Th. fasciatus*, the enlarged pharyngeal mills in *Th. mahagiensis*, *Th. albertianus* and *Th. pharyngalis*, the bullate otic region in *Th. bullatus*, the hypertrophied cephalic lateral line canals in *Th. macconneli* (and probably its near-dwarf males as well; see Greenwood, 1974*b*) and, finally, the short but broad lower pharyngeal bone in most species from the lower Zaire system. But, the restricted distribution of these apomorphic characters amongst the species obliges one to rank them either as autapomorphies or as low level synapomorphies suggesting possible intrageneric relationship (if, in the latter case, it can be shown that the characters have not evolved independently, an impossible task when there are no other features on which to establish intrageneric relationships).

Even the single synapomorphy used to define the lineage as a whole, the abrupt thoracic–flank scale size transition, is shared with *Ctenochromis* (p. 287) and *Orthochromis* (p. 296 below). The two latter lineages, however, have each their own derived features which can be interpreted as indicators of their monophyletic origin and thus their phyletic distinctiveness.

The possible interrelationships of *Thoracochromis*, *Ctenochromis* and *Orthochromis* are considered later (p. 313).

Thoracochromis has a wide but disjunct geographical distribution. In the north there are three species endemic to Lake Turkana, and two others in the Nile, both of which also occur with the three endemic species in Lake Albert. There is one species in Lake George, another in Lake Edward (with the possibility that the George species also occurs in Edward) and possibly a third in Lake Victoria.

Much further south (and a little to the west) there is one species in Lake Mweru, and a group of five species apparently confined to the lower Zaire drainage.

From an historical viewpoint (Greenwood, 1974*b*) the species of the Nile, Lake Turkana and Lake Albert could well be closely related and could also be related to the species from Lakes Edward and George. Indeed, *Th. mahagiensis* (Lake Albert) and *Th. pharyngalis* (Lake Edward) have three apparently derived characters in common, viz. hypertrophied pharyngeal mills, a low number of gill rakers (as compared with other species from Lake Albert) and a reduced cheek squamation; and again, *Th. bullatus* (Lake Albert) and *Th. macconneli* (Lake Turkana) both have hypertrophied cranial lateral line systems, although in this instance, since both species live in deep waters, the resemblance could be the result of parallel evolution.

The lower Zaire species, with the exception of *Th. demeusii*, have distinctly broad and short lower pharyngeal bones (that of *Th. demeusii* is but slightly broader than long and resembles the bone found in all other *Thoracochromis* species). *Thoracochromis moeruensis*, a geographically isolated Zairean species from Lake Mweru, also has a short and broad lower pharyngeal bone, suggesting its possible relationship with the lower Zaire species group (perhaps, geographically speaking, through some past linkage via the Kasai drainage system).

More collecting in the Zaire river system, especially its middle reaches, and more information about the northern (i.e. Nile, Turkana, Albert) species is needed before any of these suggested intralineage groups can be developed further, and indeed before the phyletic integrity of the whole lineage can be tested adequately. Data on live coloration, anal fin markings and cranial osteology are particularly needed.

The absence, save for two or possibly three species of *Thoracochromis* from the Lake Victoria–Edward–George–Kivu cichlid flock (totalling some 200 species), is of particular zoogeographical interest, especially when it is recalled that in Lakes Turkana and Albert species of *Thoracochromis* are the only '*Haplochromis*'-group taxa represented. Likewise one may note the predominance of *Thoracochromis*, *Ctenochromis* and *Orthochromis* species in the Zaire river system.

ORTHOCHROMIS Greenwood, 1954

TYPE SPECIES: *Haplochromis malagaraziensis* David, 1937 (type specimens in the Musee Royal de l'Afrique Centrale, Tervuren).

Synonymy

Rheohaplochromis Thys van den Audenaerde, D. F. E. (1963), *Revue Zool. Bot. afr.* 68, 1–2 : 145 (as a subgenus of *Haplochromis*); *idem* (1964), *Revue Zool. Bot. afr.* 70, 1–2 : 169 (raised to generic rank). No type species by original designation.

When discussing the affinities of *Rheohaplochromis*, Thys van den Audenaerde (1964 : 169) mentions my observations (*in litt.*) that the genus showed strong affinities with *Orthochromis*. Although agreeing with my remarks, Thys van den Audenaerde considered that '. . . l'écaillure nuchale et ventrale vraiment miniscule des *Rheohaplochromis* (*polyacanthus* et *torrenticola*) nous semble un caractère suffisamment important pour maintenir ces espèces dans un genre séparé . . .'. I would argue that the suite of derived characters shared by these species and the two other species discussed below (including *O. malagaraziensis*) are a stronger argument in favour of their inclusion in a single lineage of presumed monophyletic origin (i.e. within the scope of this revision, a genus see p. 269 above).

Thys van den Audenaerde's supplementary argument for placing the species *polyacanthus* and *torrenticola* together in a separate genus (because of their overlap in distribution as compared with the allopatric distribution of the other Zaire haplochromine species) might well be used to explain the presence of derived features shared only by *polyacanthus* and *torrenticola*, but it seems to have little bearing on the problem of determining their overall phyletic relationships.

In an earlier paper, Thys van den Audenaerde (1963) considered that the small ventral and nuchal scales, and the rounded pelvic fins, of *polyacanthus* and *torrenticola* could be ecophenotypic features associated with their rheophilic habits. In support of his contention he mentions similar features in *Steatocranus*, an unrelated taxon (see Greenwood, 1978). This argument of ecophenotypically evolved characters could also be used to explain the similar scale and fin characters in the two other species I would include in the same lineage as *polyacanthus* and *torrenticola*. But, to me, it would seem more parsimonious to conclude that, although the features possibly have selective advantage in a torrential habitat, their association in a number of species sharing other derived features is more likely to be indicative of common ancestry than of repeated parallel evolution. Since *Steatocranus* may well be a member of a much more distantly related branching within the African Cichlidae (see Greenwood, 1978), the similarity in scale and fin organization in that instance would, I agree, be the result of convergence (and thus indicative of the characters having adaptive value in that type of habitat).

Description

Body elongate and slender (*its depth* 25–30% *of standard length*)*; dorsal head profile strongly decurved, eyes generally suprolateral in position*, giving the fish a somewhat goby-like appearance.

Squamation. Scales on the head and on the body above the upper lateral line are cycloid or weakly ctenoid, or cycloid over the anterior third of the upper body and ctenoid over the posterior two-thirds. Scales below the upper lateral line are ctenoid except on the chest and belly, where they are cycloid.

The chest is naked or scaled (if the latter there is sometimes a small naked area on one or both sides of the body); *the chest scales, when present, are very small, as are the scales on the ventral and ventrolateral body surface as far posteriorly as the anus* (Fig. 3).

The small ventral body scales have an abrupt size transition with the moderatley larger scales on the ventrolateral aspects of the flanks. When the entire chest is scaled, the small scales of that region extend posteriorly beyond a line joining the pectoral and pelvic fin insertions (Fig. 3). *There is also a sharply defined size difference between the larger ventrolateral body scales and the small thoracic ones, the line of size demarcation curving gently in a posteroventral direction to merge with the demarcation line separating the belly and ventrolateral flank scales* (Fig. 3). *In effect, the corslet of small scales covering the chest trails backwards to the anus* (cf. *Ctenochromis* and *Thoracochromis* where the corslet is confined to an area anterior to the pelvic–pectoral fin insertions). Even when the major part of the chest is naked, there is a patch of small scales between and somewhat posterior to a line through the pelvic and pectoral fin insertions; as in the other species, these small scales are sharply demarcated from the larger ones on the flank.

The nuchal scales in two species (*O. polyacanthus* and *O. torrenticola*) are very small and deeply embedded.

There are 30–35 (modal range 30–32) scales in the lateral line, *all the pore-bearing scales of the upper lateral line being separated from the dorsal fin base by not more than one large and one small scale* (cf. *Ctenochromis* and *Thoracochromis* where only the last few scales of the upper lateral line are separated from the dorsal fin by less than two scales of equal size).

The cheek is naked or, if scaled, has a distinct naked area along its entire ventral border; in some individuals with otherwise naked cheeks, a few irregularly arranged scales may occur posterodorsally.

Neurocranium. The skull in *Orthochromis* differs from the generalized type *in having a relatively low and short supraoccipital crest, and in having the skull roof anterior to the supraoccipital crest gently rounded* (not concave or flat as is the generalized skull); *the entire neurocranium is relatively narrow, most noticeably in the interorbital region, and the preorbital skull profile slopes downwards at a steep angle.*

Vertebral numbers: 27–30 (modal range 28–30), comprising 12 or 13 (mode 13) abdominal and 14–17 (mode 17) caudal elements.

Dentition. The outer teeth in both jaws are either bicuspids (generally with the shaft of the tooth curved buccally) or slender unicuspids (in which case small fish have bicuspid teeth). Some slender unicuspids are present posteriorly in the premaxilla of all species.

Inner row teeth are small and tricuspid (with some unicuspids present when the teeth of the outer row are predominantly unicuspids), are arranged in 2 or 3 series anteriorly and laterally, and in a single row posteriorly.

Lower jaw appears foreshortened in lateral view because its posterior region (*angulo-articular bone and the coronoid process of the dentary*) *are deepened* relative to the generalized condition seen, for example in *Astatotilapia*.

Lower pharyngeal bone and dentition. The dentigerous surface of the lower pharyngeal bone is somewhat broader than it is long (*c*. 1½ times), but is not sufficiently broad to give the bone an overall short and broad appearance. The teeth are compressed and cuspidate, those of the two median rows showing some interspecific variation in form, from not as coarse or slightly coarser than the lateral teeth, to being markedly coarser; teeth forming the posterior transverse row are coarse (but cuspidate) in all species.

Dorsal fin with *16–20* (*modes 17 and 18*) *spinous* and 9–11 (modes 9 and 10) branched rays.

Anal fin with 3 or, in one species, 4 spines, and 7–10 branched rays.

Caudal fin skeleton. The occurrence of fused hypural elements (as determined from radiographs, and in the case of *O. malagaraziensis* an alizarin preparation) is as follows: in *O. malagaraziensis* (7 specimens, including 1 paratype), *O. polyacanthus* (11) and *O. machadoi* (2), hypurals 1 and 2, and 3 and 4 are fused, but in *O. torrenticola* (2) none is fused although all are closely apposed to one another in each half of the skeleton. Vandewalle (1973) records no fusion in the specimen of *O. torrenticola* he examined.

Caudal fin is moderately to strongly subtruncate (almost rounded).

Pelvic fin with the second, or the second and third branched rays the longest, thus giving the fin a rounded rather than an acute distal margin.

Anal fin markings in male fishes. No discrete, egg-dummy-like markings have been described for any *Orthochromis* species, nor are any visible in the preserved material examined; certainly none was visible in the live specimens of *O. malagaraziensis* I examined (Greenwood, 1954). In some species the fin is without any form of maculate colour pattern so that if egg-dummies were present they should be visible. *Orthochromis torrenticola* does have a maculate anal fin (the spots arranged in oblique rows) and Thys van den Audenaerde (1963) reports that males have more densely spotted fins that do females.

Observations on live *O. malagaraziensis* suggest that sexually dimorphic coloration in that species may be confined to differences in the colour of the lips, anal fin, and branchiostegal membrane (Greenwood, 1954).

Gill rakers relatively slender but short, 6–9 (modes 7 and 8) in the outer row on the lower part of the first gill arch.

Contained species

Orthochromis malagaraziensis (David), 1937. Malagarasi river (Burundi and Tanzania); see Greenwood (1954) for a redescription of the species and notes on its biology.

Orthochromis polyacanthus (Blgr.), 1899. Lake Mweru, Upper Zaire river (Stanley Falls and Stanleyville, and certain affluent rivers (see Thys van den Audenaerde, 1963)). I have, for the moment, accepted Regan's (1922*a*) synonymy of Boulenger's (1902) *Tilapia stormsi* with this species; however, a review of material in the BMNH suggests that Regan's opinion may not be correct.

Orthochromis torrenticola (Thys van den Audenaerde), 1963. Lufira river (Upper Zaire river drainage).

Orthochromis machadoi (Poll), 1967. Cunene river, Angola.

Diagnosis and discussion

Members of the genus *Orthochromis* are characterized, principally, by the abrupt size change between the large scales on the ventrolateral aspects of the flanks and the small scales of the chest and belly, by the curved and posteroventrally directed line of size demarcation between these scales, and the union of this line with that separating the very small scales on the belly from the larger scales on the flanks, see Fig. 3. The very small belly scales, extending backwards to the anus, are another characteristic feature. Also characteristic (when taken in combination with those characters listed above) is the absence or extensive reduction of the cheek squamation, the posteriorly deepened lower jaw, the increased number of spinous rays in the dorsal fin (without a corresponding reduction in the number of branched rays, this comparison being based on the modal counts for branched rays in *Ctenochromis* and *Thoracochromis*), the elongate second or second and third branched rays in the pelvic fin and, apparently, the absence of egg-dummy-like markings on the anal fin of adult males.

Other diagnostic features are reviewed on pp. 295–296 above; the high frequency of hypural fusion, affecting both the upper and lower halves of the caudal fin skeleton, is particularly noteworthy but requires confirmation from larger samples and the use of skeletal rather than radiographed material.

The absence of egg-dummy-like markings on the anal fin also requires confirmation from observations made on live specimens (their absence in *O. malagaraziensis*, however, seems certain; Greenwood (1954)). This is a most unusual feature amongst '*Haplochromis*'-group species, and may imply that the courtship and breeding habits of *Orthochromis* species are also unusual for the group. Until something is known about these habits in *Orthochromis* it is impossible to determine whether the absence of egg-dummies is to be considered a primitive or a derived feature for the genus.

I am unable to demonstrate any clear-cut interspecific relationships within the *Orthochromis* lineage. *Orthochromis machadoi* (Cunene river) is probably the least derived member. It has a partly scaled cheek, the chest is either entirely scaled or, as in one specimen, it can have a small scaleless area unilaterally, the ventral (belly) body scales are relatively large and, finally, in its general facies the species has not fully achieved the elongate goby-like body form seen in the other species.

In his original description of *O. machadoi*, Poll (1967) argues that the species is closely related to *Pseudocrenilabrus philander* (Weber) an opinion I cannot accept (especially since Poll's views are, it seems, largely based on supposed similarities in coloration). Anatomically, and with regard to their squamation patterns, the taxa are quite distinct.

The preserved colours of *O. machadoi*, on the other hand, are like those of *O. malagaraziensis*. Both species have all the body scales (except on the chest and belly) narrowly outlined in black, giving the body an overall 'diamond-mesh' pattern; they also have a distinctive and vertically elongate dark blotch at the base of the caudal fin.

In *O. torrenticola* this diamond-mesh pattern is very faint but general over the body, whereas in *O. polyacanthus* it is restricted to a pair of narrow bands, one situated midlaterally, the other following the upper lateral line. *Orthochromis torrenticola* retains the caudal spot which is lost in *O. polyacanthus*. Both species have the body crossed by several closely spaced vertical bands. The apo- or plesiomorph states of these colour patterns cannot be determined.

Orthochromis torrenticola and *O. polyacanthus* have minute scales on the dorsal surface of the head and nuchal region (in *O. machadoi* and *O. malagaraziensis* these scales are only slightly smaller than those on the dorsal body surface), and the scales on the thoracic region are relatively smaller than in the other two species, especially *O. machadoi*. In other words, *O. torrenticola* and *O. polyacanthus* share derived features in their squamation.

If these various characters can be taken as indicators of relationship, then *O. machadoi* and *O. malagaraziensis* would be sister species, as would *O. torrenticola* and *O. polyacanthus*. But, one must set against these similarities the fact that the chest and cheek are naked (or largely naked) in *O. malagaraziensis* and *O. torrenticola*, and that both species have similar general facies (sharply decurved anterior head profile, elongate body and a suprolateral eye), all features which would appear to be derived rather than plesiomorph ones. The four anal spines in *O. torrenticola* must be considered an autapomorphic feature and as such cannot be used to assess relationships.

Orthochromis, *Ctenochromis* and *Thoracochromis* share one derived feature, the abrupt size transition between chest and body scales, and thus are presumed to be derived from a common ancestor also possessing this feature. However, no synapomorph character can be found to indicate which two of the three genera are more closely related to one another.

Since *Thoracochromis* has only one apomorph feature (chest–body scale size transition), a character shared by all three taxa, it can on that basis be considered to represent the least derived member of the group.

Ctenochromis and *Orthochromis* both exhibit, but do not share, a number of derived features which must, therefore, be considered autapomorphic for the lineage in which they occur (and define). If one were to consider 'trend' characters, for example a tendency to reduce cheek and chest squamation, then *Ctenochromis* and *Orthochromis* could be said to share some derived features not shared with *Thoracochromis*. But, I can find no trenchant synapomorphic character that would allow one to establish an unequivocal sister-group relationship between the two taxa. It is for this reason that I have given each lineage in this ultimately monophyletic assemblage the status of a genus (see p. 269) rather than ranking *Orthochromis* and *Ctenochromis* as subgenera (i.e. implicit sister-groups) on the grounds of their having shared and presumed apomorph 'trend' characters.

Section II

Although several of the species dealt with in this section have previously been referred to the genus *Haplochromis* (see Bell-Cross, 1975), at least one author (Trewavas, 1964) has suggested that these same species, together with the genera *Serranochromis* and *Chetia*, are more closely related to one another than to any of the species already accounted for. In part I would agree with Trewavas' groupings, but the available evidence does not allow one to substantiate, in their entirety, the relationships indicated in her phyletic diagram (Trewavas, 1964 : fig. 1), nor is it possible to determine the relationships of these 'southern' taxa with the more northern '*Haplochromis*'-group genera considered in Section I.

SERRANOCHROMIS Regan, 1920

TYPE SPECIES. *Chromys thumbergi* Castelnau, 1861 (neotype, designated by Trewavas (1964), in BMNH collections).

I have united several species (those previously placed in this genus by Trewavas (1964) and others placed in *Haplochromis* by Bell-Cross (1975)) into one lineage (=genus) because all share the following apparently derived features: (i) *A high number of abdominal vertebrae*, 16–18, *rarely* 15 *or* 19 (*modal numbers* 16 *and* 17). (ii) *A large number of gill rakers*, 9–15 (*modal range* 10–13) *in the outer row on the lower part of the first gill arch.* (iii) *A high number of branched fin rays in the dorsal fin.*

In addition, members of this lineage reach a large adult size, all have cycloid or a mixture of cycloid and weakly ctenoid scales (the ctenii confined to a small median sector on the scale's posterior margin) in which the cycloid kind predominate, and the anal fin markings (egg-dummies) in males are numerous, small and non-ocellate (in some species differing little in size, shape or colour from the spots on the soft part of the dorsal fin). It is not, however, possible to assess the primitive or derived states of these features which, therefore, are of no direct value in assessing phylogenetic affinities, (but see p. 274 regarding egg-dummies.)

Two sublineages, each based on shared derived features common to their constituent species, can be recognized within the genus *Serranochromis*, and these are given subgeneric rank.

Subgenus *SERRANOCHROMIS* Regan, 1920

TYPE SPECIES. *Chromys thumbergi* Castelnau, 1861.

Description

The body form varies from deep to moderately slender (body depth 30–45% of standard length).

Squamation. The scales on the head, chest, cheek and above the upper lateral line are cycloid, those elsewhere on the body mostly cycloid. When ctenoid scales are present these are weakly ctenoid, with the ctenii confined to a short median sector on the free margin of the scale.

The scales on the chest (which may be relatively small) show a gentle size gradation with those on the lateral and ventrolateral aspects of the flanks; the chest is always fully scaled.

The cheek is fully scaled, *with from* 3 (*rare*) *to* 11 *horizontal rows of scales* (*usually* 5–9 *rows*).

There are 35–41, *rarely* 34 *scales in the lateral line*, all but the last 2 or 3 pore-bearing scales of the upper lateral line are separated from the dorsal fin origin by two scales of approximately the same size.

Neurocranium. The skull has a protracted preotic region (*comprising some* 65–70% *of the total neurocranial length*), *especially noticeable in the ethmovomerine region which comprises c.* 27–33% *of the total neurocranial length. The ethmovomerine part of the skull is almost horizontally aligned, its dorsal surface sloping at a small angle* (*Fig. 13*). The supraoccipital crest is variously developed, high in some species, relatively lower in others but never shallow relative to the total skull proportions.

Vertebral numbers and apophysis for the dorsal retractor muscles of the upper pharyngeal bones. *There are* 31–36 *vertebrae, comprising* 16–18, *rarely* 15 *or* 19 (*modes* 16 *and* 17) *abdominal and* 16–18, *rarely* 15 (*modes* 16 *and* 17) *caudal elements.* Such a high number of both caudal and abdominal vertebrae is rarely encountered amongst '*Haplochromis*'-group cichlids, and is unique amongst the fluviatile taxa (see, also p. 313 below).

An apophysis for the origin of the dorsal retractor muscles of the upper pharyngeal bones is developed on the ventral face of either the 3rd or 4th abdominal vertebra; although the apophysis does occur on the 4th vertebra in other '*Haplochromis*'-group taxa, it is usually confined to the 3rd centrum (see Trewavas, 1964 for comments on this feature).

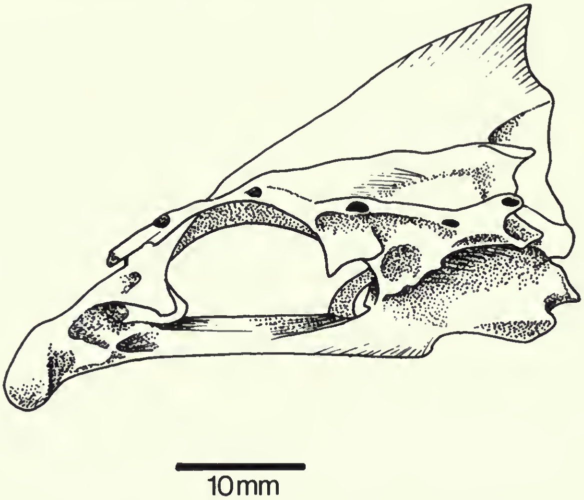

Fig. 13 Neurocranium of *Serranochromis* (*Serranochromis*) *robustus*; left lateral view.

Dentition. The teeth in both the inner and the outer rows of the jaws are unicuspid, even in the smallest (29 *mm SL*) *specimens examined.* Other '*Haplochromis*'-group species in which the adult dentition is a unicuspid one (and for which specimens less than 100 mm SL are available), have bicuspid outer teeth, and usually tri- or bicuspid inner teeth, in fishes less than 80–100 mm standard length.

The inner teeth are arranged in a single (*rarely a double*) *row; when two rows are present, these are confined to the anteromedial part of the jaw, the series continuing posteriorly as a single row. In many species the inner teeth of the lower jaw are confined to a narrow, anteromedial arc.* The majority of '*Haplochromis*'-group taxa have a more extensive inner dental pattern, with the teeth arranged in at least 2 (and usually 3) rows over the anteromedial and anterolateral parts of the jaw bones.

Lower pharyngeal bone and teeth. With regard to its outline shape when viewed occlusally, two kinds of pharyngeal bone can be recognized (Fig. 14). *In one, the commoner type, the bone is long and narrow, the dentigerous surface having the outline of an isosceles triangle* (Fig. 14A & B). The second type (found in two species) is relatively broader and its dentigerous surface, although still slightly broader than long (*c.* $1\frac{1}{3}$ times) is more nearly equilateral (Fig. 14C).

Irrespective of the bone's outline shape, the teeth (except those in the two median rows) are fine and either simply pointed or with a weakly developed shoulder anterior to the pointed cusp. The two median and the posterior transverse rows are made up of stouter teeth, those in the median rows are relatively the stouter and have the shoulder more clearly demarcated than it is in the outer teeth.

Jaws. The lower jaw is relatively slender in lateral view (Fig. 15B) and is not noticeably deepened posteriorly (angulo-articular region). *The premaxillae have, in most species, long ascending pro-*

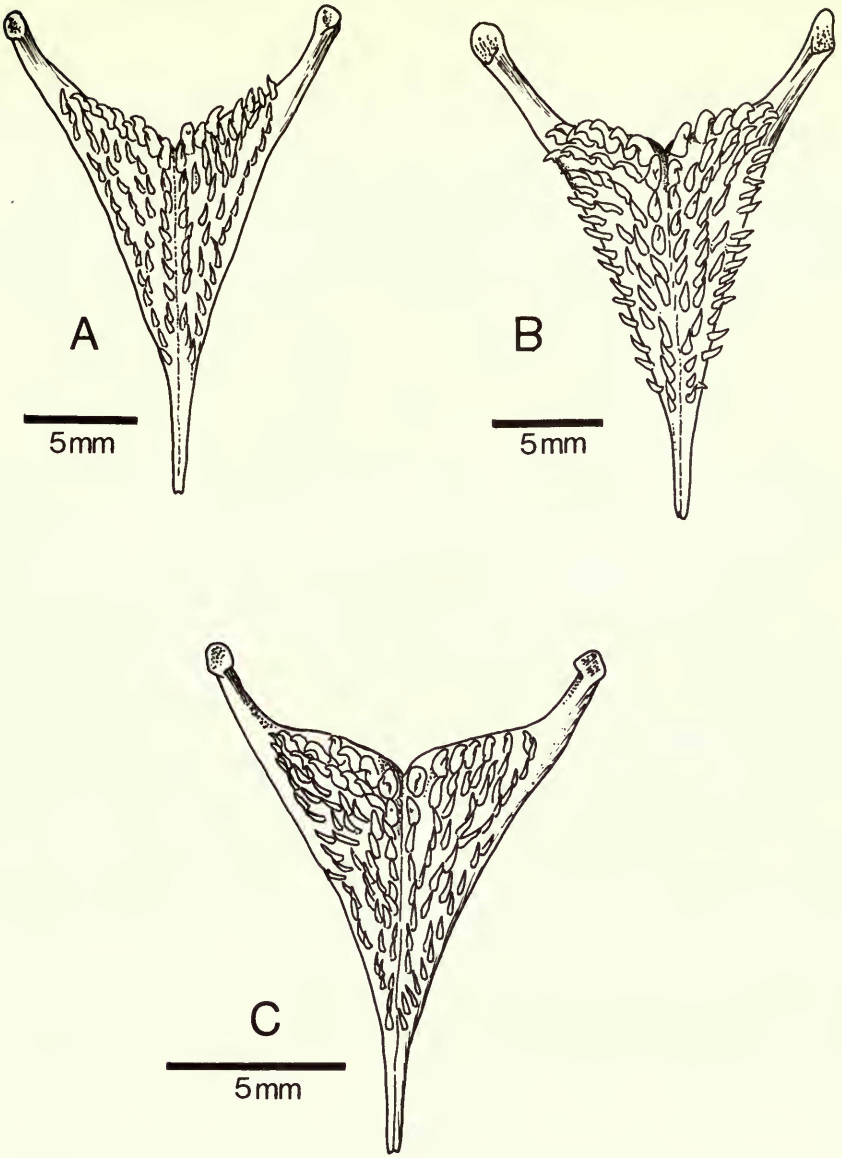

Fig. 14 Lower pharyngeal bones of various *Serranochromis* (*Serranochromis*) species, seen in occlusal view. A. *Serranochromis* (*S.*) *thumbergi.* B. *S.* (*S.*) *robustus.* C. *S.* (*S.*) *macrocephalus.*

cesses (Fig. 15A) *which, in the entire fish, extend to the level of the midpoint of the dorsal orbital margin or even further dorsoposteriorly.*

Dorsal fin: with 13–18 (modes 15 and 16) spinous, and 13–16 (*usually* 14–16) *branched rays* (a high branched ray count when compared with that in other fluviatile haplochromine taxa).

Anal fin: with 3 spines and *9–13* (*modes 10 and 11*) *branched rays* (again, a high branched ray count).

Caudal fin skeleton. No hypural fusion was noted in any of the radiographed material examined, i.e. *S. macrocephalus* (12 specimens), *S. spei* (1), *S. robustus* (14), *S. longimanus* (4), *S. angusticeps* (17), *S. stappersi* (1), *S. meridionalis* (1). No fusion was reported by Vandewalle (1973) in the *S. macrocephalus* (1) or *S. robustus* (1) he examined.

Caudal fin: subtruncate (slightly emarginate in one species) to weakly rounded.

Pelvic fin: with the first branched ray the longest.

Anal fin markings in male fishes. Most species have many small, generally circular spots without a clear surround and covering a large area of the soft anal fin, sometimes extending onto the spinous part as well. In their size and shape these spots are similar to those on the soft part of the dorsal fin and on the caudal fin. An exception to these generalizations is *S. spei* which has fewer and larger (but non-ocellate) spots covering the greater part of the soft fin.

From the little information available on live coloration it seems possible that the anal spots may differ slightly from the dorsal fin spots in colour and intensity, but this requires confirmation. (For coloured illustrations, see Jubb (1967*a*, pls 41–44) and Bell-Cross (1976: pls 26–28).

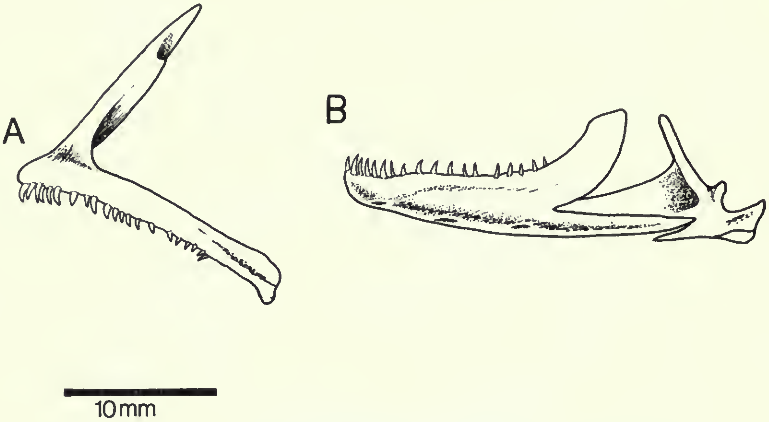

Fig. 15 Jaws of *Serranochromis* (*S.*) *robustus*; left lateral view. A. Premaxilla, B. Lower jaw.

Trewavas (1964) reports that similar spots are present on the anal fin of females, but are grey rather than red, yellow or orange as in males.

Where breeding habits are known, the species are female mouthbrooders.

Gill rakers are of various forms, from short and stout to moderately slender; there are 9–13 (modal range 10–12) rarely 8 rakers in the outer row on the lower part of the first gill arch.

Contained species

See Trewavas (1964) for detailed descriptions, figures, etc.

Serranochromis (*S.*) *robustus* (Günther), 1864. Lake Malawi, Upper Shire river; Mossamedes; Okavango; Upper Zambesi; Kafue river; Luangwa system (tributary of the Middle Zambesi); Bangweulu region; Luembe river, Kasai system (see Poll, 1967); possibly also in Lake Mweru and the Lualaba system.

Serranochromis (*S.*) *thumbergi* (Castelnau), 1861 (Type species). Mossamedes; Okavango river and Lake Ngami; rivers Kafue and Luansemfwa (Luangwa system); Bangweulu region; Upemba basin.

Serranochromis (*S.*) *macrocephalus* (Blgr.), 1899. Mossamedes; Okavango river; Lake Cameia (on an Angolan tributary of the Upper Zambesi); Upper Zambesi; Kafue river; Luansemfwa river, Luangwa system; Luapula river; Lake Mweru; Lulua river; Angolan Kasai.

Serranochromis (*S.*) *angusticeps* (Blgr.), 1861. Mossamedes; Okavango river and Lake Ngami region, Upper Zambesi; Kafue river; Bangweulu region; Luapula river; possibly Lake Mweru (see also Poll, 1967).

Serranochromis (*S.*) *longimanus* (Blgr.), 1911. Okavango river and the Upper Zambesi.

Serranochromis (*S.*) *stappersi* Trewavas, 1964. Lake Mweru and the lower Luapula river.

Serranochromis (*S.*) *spei* Trewavas, 1964. Lake Kafakumba (23°40′ E, 9°40′ S) on a tributary of the Kasai system; Lake Kabongo in the Lake Upemba depression.

Serranochromis (*S.*) *janus* Trewavas, 1964. Malagarasi swamps (Malagarasi river), Tanzania.

Serranochromis (*S.*) *meridionalis* Jubb, 1967. Incomati river system, Transvaal, South Africa (see Jubb, 1967*b*).

Dr Trewavas (1964) has discussed the possible affinities of these species (except *S. meridionalis*) at what should now be considered an intra-subgeneric level. Until more material is available for anatomical studies no further comment would be worthwhile. The relationships of the subgenus with its sister-group (*Sargochromis*), and of the genus as a whole, will be considered below (p. 306).

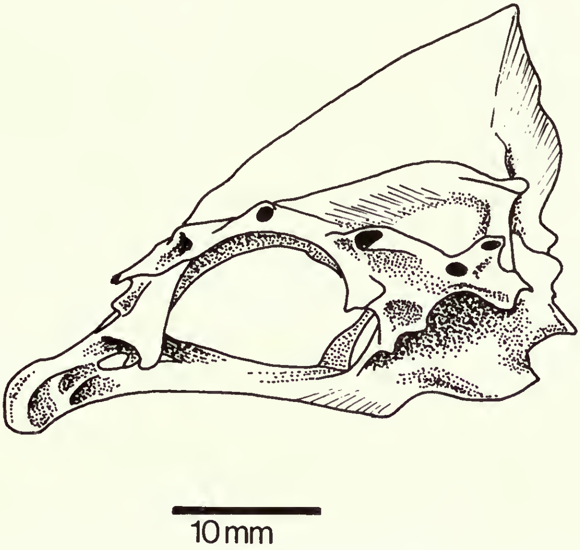

Fig. 16 Neurocranium of *Serranochromis* (*Sargochromis*) *codringtoni*; left lateral view.

Subgenus ***SARGOCHROMIS*** Regan, 1920.

TYPE SPECIES: *Paratilapia codringtoni* Blgr., 1908 (type specimen in the collections of the BMNH, see Bell-Cross, 1975).

Description

Body deep and stout (depth 35–50% of standard length).

Sargochromis differs from the nominate subgenus in the following characters:

Squamation. There are fewer lateral line scales (28–34, modes 30 and 31, cf. 35–41 rarely 34).

Neurocranium. Although basically of the same type as that in *Serranochromis*, most *Sargochromis* species have a somewhat shorter ethmoid region (but similar preotic skull proportions), a deeper otico-occipital region and, in some species, a more robust apophysis for the upper pharyngeal bones (Fig. 16). This latter character is positively correlated with the degree of enlargement of the pharyngeal bones and the extent to which their dentition is molarized (see Greenwood, 1965*a* and 1978). The more massive the pharyngeal bones the greater is the relative contribution of the basioccipital to the articular surface of the apophysis, and in those species with the largest bones the prootic also contributes to that surface.

Vertebral numbers. There are fewer caudal vertebrae (12–16, modal numbers 14 and 15), and hence a lower total count (28–32, mode 31). *The number of abdominal vertebrae*, however, *is high* in both subgenera.

Jaws. The dentary differs from that in *Serranochromis* in being relatively more foreshortened and thus deeper (Fig. 17). The premaxillary ascending processes do not extend beyond about the midpoint of the anterior orbital margin (beyond that point in most *Serranochromis*).

Dentition. Unlike small specimens of *Serranochromis*, small *Sargochromis* do have some bicuspid inner and outer teeth (at least some specimens $<$ 10–15 cm, depending on the species, have predominantly bicuspid outer teeth). The dental pattern is similar in both subgenera, save that *S.* (*Sargochromis*) *thysi* has 4 inner series in both jaws.

Lower pharyngeal bone and teeth. The bone shows some interspecific variation in outline shape (Fig. 18) but is always relatively broader than in *Serranochromis*, and thus the dentigerous surface more closely approximates to the equilateral. In only one species, *S.* (*Sargochromis*) *greenwoodi* (Fig. 18A), are there no markedly enlarged median teeth. Most of the other species have some enlarged, often submolariform, teeth in addition to those forming the two median rows. Generally these enlarged teeth are restricted to a central patch, several tooth rows wide, in the posterior (oesophageal) dentigerous field. Two species, *S.* (*Sargochromis*) *codringtoni* and *S.* (*Sa.*) *giardi*, have most of the pharyngeal dentition composed of coarse, molariform or submolariform teeth.

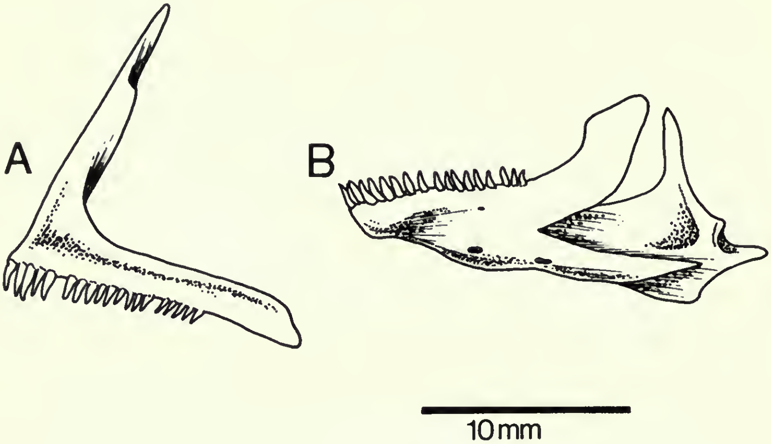

Fig. 17 Jaws of *Serranochromis* (*Sargochromis*) *codringtoni*; left lateral view. A. Premaxilla, B. Lower jaw.

Bell-Cross (1975 : fig. 1) described intrapopulational differences in the extent to which the pharyngeal dentition is enlarged.

Most *Sargochromis* species have the lower pharyngeal bone coarser than it is in the nominate subgenus, and markedly so when the pharyngeal dentition is hypertrophied.

Dorsal fin has a lower modal branched ray count (12 or 13 cf. 14–16 in *Serranochromis*) but there is an extensive overlap in the total ranges (11–16 cf. 13–16). There is also a broad overlap in spinous ray counts, although the higher numbers (17 and 18) recorded for the nominate subgenus have not been reported for *Sargochromis*.

Anal fin markings are essentially the same in both subgenera. For colour illustrations see Jubb (1967*a* : pls 40 and 45); Bell-Cross (1976 : pls 17 and 18).

Caudal fin skeleton. No hypural fusion was seen in the radiographs of *S.* (*Sa.*) *coulteri*, *S.* (*Sa.*) *greenwoodi*, and *S.* (*Sa.*) *codringtoni* (1 specimen each); in *S. carlottae* one specimen has hypurals 3 and 4 fused but two other fishes show no fusion. Of the two *S.* (*Sa.*) *mellandi* examined, one has hypurals 3 and 4 fused, but the other has none fused. Vandewalle (1973) records *S.* (*Sa.*) *mellandi* as having either no fusion (4 specimens) or hypurals 3 and 4 fused (2 specimens).

Caudal fin strongly subtruncate to virtually rounded.

Gill rakers are more numerous in *Sargochromis* (9–15, modal numbers 12 and 13).

Contained species

For a systematic review and notes on the ecology and distribution of the first seven species listed below see Bell-Cross (1975).

Serranochromis (*Sa.*) *greenwoodi* (Bell-Cross), 1975. Upper Zambesi; Kafue system; Okavango system.

Serranochromis (*Sa.*) *coulteri* (Bell-Cross), 1975. Upper Cunene system.

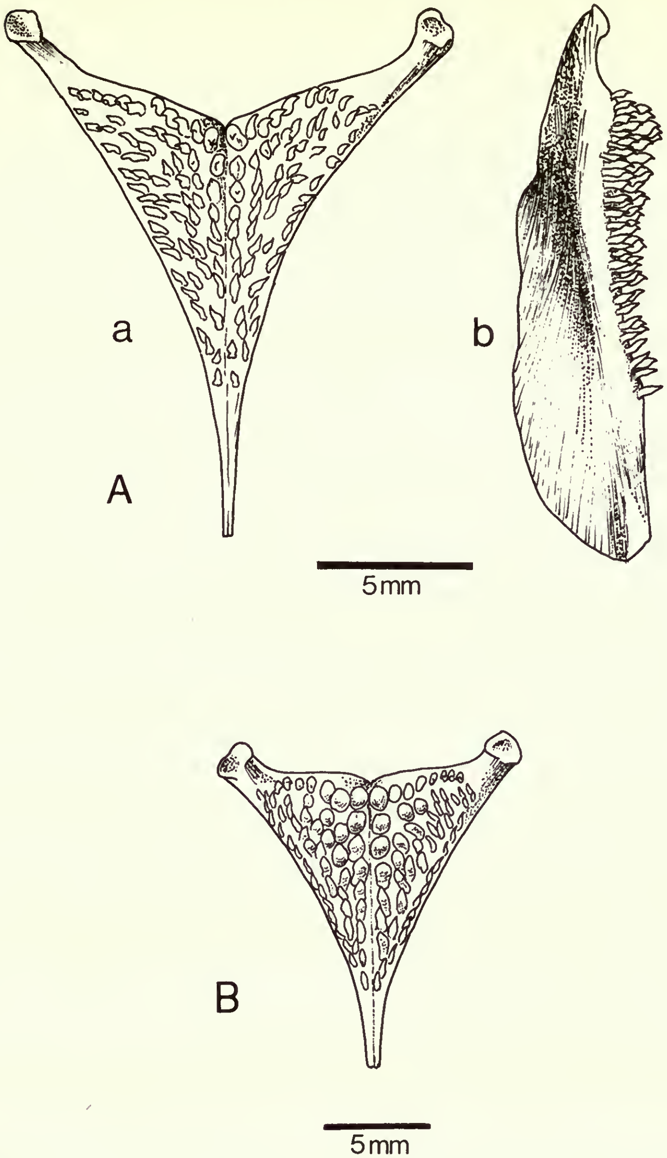

Fig. 18 Lower pharyngeal bone of : A. *Serranochromis* (*Sargochromis*) *greenwoodi* in a. Occlusal, and b. Right lateral view (bone aligned vertically). B. *S.* (*Sa.*) *codringtoni*; occlusal view.

Serranochromis (*Sa.*) *mortimeri* (Bell-Cross), 1975. Upper Zambesi; Kafue river (above the Lufwanyama–Kafue confluence); part of the Mulungishi river (a Middle Zambesi tributary).

Serranochromis (*Sa.*) *mellandi* (Blgr.), 1905. Chambesi river and Lake Bangweulu; the Luapula river and Lake Mweru; Lake Calundo, Angola (see Poll, 1967).

Serranochromis (*Sa.*) *carlottae* (Blgr.), 1905. Upper Zambesi; Okavango and Kafue systems.

Serranochromis (*Sa.*) *codringtoni* (Blgr.), 1905 (Type species of the subgenus). Upper and Middle Zambesi rivers (including the larger tributaries); Kafue and Okavango river systems.

Serranochromis (*Sa.*) *giardi* (Pellegrin), 1904. Middle and lower regions of the Upper Zambesi; the Okavango and the plateau section of the Kafue river; one record from the Cunene system.

Serranochromis (*Sa.*) *thysi* (Poll), 1967. Luembe river, Angola.

Diagnosis and discussion

Members of both subgenera comprising the genus *Serranochromis* are characterized by having a high modal number of abdominal vertebrae (16 or 17, rarely 15 or 19, modes 16–18) and thus a high total vertebral count (29–36), a high number of gill rakers in the outer row on the lower part of the first gill arch (10–15, rarely 9, modal range 10–13), a generally high number of branched dorsal fin rays (11–16, modal range 12–16), mostly cycloid scales on the body (if some ctenoid scales are present they are weakly so), a high number of lateral line scales (28–41) as compared with other fluviatile '*Haplochromis*'-group species and, at least in one subgenus, a greater number of scale rows on the cheek (5–9), in having a skull with a relatively protracted preotic region and relatively high supraoccipital crest, and in having numerous, small non-ocellate coloured spots on the anal fin of male fishes (these markings differing but slightly in size and colour from those on the dorsal fin).

Diagnostic features for the two subgenera are detailed on pp. 299–301 & 303–304, and in the key (p. 316). They involve, chiefly, the higher number of caudal vertebrae and branched dorsal fin rays in *Serranochromis* (*Serranochromis*) species, and the stouter lower pharyngeal bones and dentition in *Serranochromis* (*Sargochromis*) species.

Trewavas (1964) and Bell-Cross (1975) have considered intragroup relationships within the subgenera *Serranochromis* and *Sargochromis* respectively. A reconsideration of their conclusions is beyond the scope of this paper, although Trewavas' (1964 : fig. 1 and p. 10) grouping of the *Serranochromis* (*Serranochromis*) species would seem, on the basis of the characters used, to be a sound hypothesis.

Trewavas (1964) also made an extensive analysis of the intergroup (i.e. intergeneric) relationships of what I am treating as the subgenus *Serranochromis* (treated by Trewavas as a genus). She brought into these considerations the 'genus' *Sargochromis* (*S. codringtoni* only) and three '*Haplochromis*' species (*mellandi*, *frederici* and *carlottae*) which are now referred to *Sargochromis* (as a subgenus of *Serranochromis*). In discussing Trewavas' ideas, unless quoting directly, I shall use the terms '*Serranochromis*', '*Haplochromis*' and '*Sargochromis*' to cover her concept of these taxa.

In Trewavas' view (1964 : also fig. 1, p. 8) '*Serranochromis*' is '. . . a gradal genus rather than a clade', of diphyletic origin from '. . . a small species-flock of *Haplochromis*' (i.e. the four *Haplochromis* of Angola, '*H*'. *lucullae*, '*H*'. *humilis*, '*H*'. *acuticeps* and '*H*'. *angolensis*, plus '*H*'. *darlingi* of the Zambesi (see below, pp. 310–313).

'A cladal grouping,' Trewavas continues, 'would recognize *Chetia*, *S. robustus* and *S. thumbergi* on the one hand, and *H. welwitschii*, *S. macrocephalus* and the other species of *Serranochromis* on the other, but definitions would be almost impossible. . . . The broken line' (referring to fig. 1) 'at the *Haplochromis–Sargochromis* transition reflects the absence here too of a clear generic division'.

Because all '*Serranochromis*' species share a high caudal vertebral count and other apparently derived features (see p. 299), I cannot accept Trewavas' concept of that taxon having a diphyletic origin, nor can I accept, without considerable qualification, the inclusion of *Chetia* (i.e. *C. flaviventris*) and '*H.*' *welwitschii* in one cladal grouping. Neither *Chetia* nor '*H.*' *welwitschii* has the high caudal vertebrae count of '*Serranochromis*' (i.e. the nominate subgenus recognized above) and, although these two species together with certain other endemic Angolan '*Haplochromis*' and '*H.*' *darlingi* do share some features with *Serranochromis*, these are not of the kind that would suggest a close cladistic relationship.

The question of possible relationships between the Angolan species, '*H.*' *darlingi* and *Chetia flaviventris* will be considered on pp. 312–313.

Trewavas (1964 : fig. 1, p. 9) recognizes the phyletic affinity between *Serranochromis* and *Sargochromis* (the latter now of course broadened to include the three '*Haplochromis*' (see p. 305) species which she indicated as being more closely related to '*Sargochromis*' than '*Serranochromis*'). We would differ, however, in our interpretation of the relationship between *Sargochromis* and '*Haplochromis*' *darlingi*. Trewavas (1964 : 9) writes of 'The evolutionary line which leads from *H. darlingi* to *Sargochromis* . . .' But I can find only one derived character (the enlarged pharyngeal mill) that might link '*darlingi*' more closely with *Sargochromis* than with *Serranochromis*, and none of the synapomorph characters shared by *Serranochromis* and *Sargochromis* alone. In the absence of these characters from '*H.*' *darlingi*, and because an enlarged pharyngeal mill has apparently evolved independently in several haplochromine lineages, I consider that the affinities between this species and *Serranochromis* (including *Sargochromis*) are not as close as those implicit in Trewavas' proposed ancestor–descendant relationship.

In my view, *Serranochromis* and *Sargochromis* shared a recent common ancestry not shared with '*H.*' *darlingi* (the common ancestor for the former taxa could well have resembled *S.* (*Sa*) *greenwoodi* in its anatomical, morphological and meristic features; see description in Bell-Cross, 1975).

Any relationship between the genus *Serranochromis* and '*H.*' *darlingi* would be at a more distant level because these two taxa share fewer derived features than do *Serranochromis* and *Sargochromis*.

Finally, comment must be made on the superficially close resemblance between members of the subgenus *Serranochromis* (*Serranochromis*) and certain '*Haplochromis*' species of Lake Victoria (the *spekii–serranus* species complex, see Greenwood, 1967 : 109, and 1974*a* : 80 *et seq.*; also Trewavas, 1964 : 6). That the resemblance is the result of convergent evolutionary trends towards the production of an adaptive morphotype (piscivorous predator) and not one of close phyletic relationship seems evident from the several features in which the two taxa differ from one another. For example, the predominantly cycloid and weakly ctenoid scales of *Serranochromis* compared with the strongly ctenoid scales of the '*Haplochromis*' species, the few and fully ocellate egg-dummies of the latter as contrasted with the numerous, small and non-ocellate anal spots in *Serranochromis*, and the more numerous gill rakers, branched fin rays and, particularly, the high number of abdominal vertebrae in the latter taxon.

Certainly it would seem more parsimonious to suppose that *Serranochromis* and the Lake Victoria *Haplochromis* were derived from different lineages, rather than to suggest a common ancestry from some widespread lineage of fluviatile, piscivorous predators (an idea I had entertained previously when considering the phyletic history of the Lake Victoria species flock).

It would seem possible, too, that there is no close phyletic relationship between *Serranochromis* and certain '*Haplochromis*' species in Lake Malawi (see Trewavas, 1964 : 6), but more research is required on the Malwai species before this idea can be tested adequately.

CHETIA Trewavas, 1961.

TYPE SPECIES. *Chetia flaviventris* Trewavas, 1961 (Holotype and paratypes in the BMNH, 3 paratypes in the Transvaal Museum, Pretoria).

NOTE. The species *Chetia brevis* Jubb, 1968 is excluded from this genus because in adult males the anal fin markings are large, true ocelli and few in number (3 or 4). Also, unequally bicuspid outer jaw teeth are still present in specimens of a size (86–89 mm SL) when, in *Chetia flaviventris*, the outer row is comprised mainly of unicuspid and caniniform teeth; the few bicuspid teeth present in *C. flaviventris* of that size are different from those in *C. brevis* since the minor 'cusp' is a shoulder and not a point.

Description

The body form is moderately slender (depth of body 29–35% of standard length).

Squamation. The scales on the head, chest, cheek and body above the upper lateral line are cycloid, and cycloid scales predominate on the body below that level as well; a few weakly ctenoid scales may be present anteriorly on the body, the ctenii on these scales being confined to a short median arc on the scale's free margin. It seems possible that a higher proportion of ctenoid scales is present in smaller than in larger individuals; the largest specimen examined has only cycloid scales on all parts of the body and head (see also Trewavas, 1961).

The cheek is completely scaled (*5 or 6 horizontal rows*). The chest scales show a gentle size gradation with those on the belly and ventrolateral aspects of the flanks.

There are 34 *or* 35 *scales in the lateral line series*, with only the last one or two pore-bearing scales of the upper lateral line separated from the dorsal fin base by less than two scales of almost equal size.

Neurocranium. The skull has a moderately produced preotic region (*c*. 68–70% of total neurocranial length). The ethmovomerine region is not noticeably extended, *and slopes at a slight angle*. In its proportions and general shape, the neurocranium in *Chetia* approaches that in the subgenus *Serranochromis* (*Serranochromis*), but has a less elongate ethmovomerine region.

Vertebral numbers and apophysis for the dorsal retractor muscles of the upper pharyngeal bones. There are 30–32 (mode 31) vertebrae, comprising 14 or 15 (mode 15) abdominal and 15–17 (modes 16 and 17) caudal elements.

Trewavas (1961) reports an absence of any bony apophysis for the origin of the pharyngeal muscles; from the radiographs I have examined (i.e. of the holo- and 4 paratypes) the structure is visible in one specimen. Trewavas (1961) implies that the apophysis serves principally for the attachment of the swimbladder. That organ certainly is attached to the posterior face of the apophysis in all cichlids I have examined, but the greater surface area of the apophysis serves as a point of origin for the pharyngeal retractor muscles.

Dentition. Unicuspid teeth predominate (*or are the only kind of teeth present*) *in specimens more than* 30 *mm standard length; the few bicuspid teeth present have a much reduced, shoulder-like minor cusp, and are mostly replaced by unicuspids in specimens* $>$ 35 *mm S.L.* There is, however, a size correlated change in the kind of unicuspid teeth present. Fishes $<$ 35 mm long have rather flattened, almost spear-shaped unicuspids whereas in larger fishes the teeth are caniniform.

Unicuspid teeth also predominate in the inner rows of fishes at all sizes, although a few weakly bicuspid teeth are present in specimens less than 40 mm SL. *There are one, or, less commonly, two rows of inner teeth anteriorly in both jaws, and a single series laterally.*

Lower and upper jaws. The lower jaw has the appearance and proportions of that in *Serranochromis* (*Serranochromis*) species, but in the upper jaw the ascending premaxillary process does not reach to between the orbits as it does in many of the latter species; it reaches only to about the midpoint of the anterior orbital margin.

Lower pharyngeal bone and teeth. The bone is not thickened, has an almost equilateral dentigerous surface, and its teeth are slender and weakly cuspidate (Fig. 19). Those teeth forming the two median rows and the posterior transverse row are slightly coarser than their congeners.

Dorsal fin with 14 or 15 spinous and 11 or 12 branched rays.

Anal fin with 3 spines and 9 or 10 branched rays.

Caudal fin skeleton. All the hypurals are free in the five specimens radiographed (the type series).

Caudal fin is subtruncate.

Pelvic fin has the first branched ray the longest.

Anal fin markings in male fishes. As in *Serranochromis* (see p. 302) there are numerous, small and non-ocellate spots covering a large area of the soft anal fin, the spots resembling in size and coloration those on the soft part of the dorsal fin.

According to Du Plessis & Groenewald (1953) the anal spots in *C. flaviventris* are more plentiful in males than in females, and the species is a female mouthbrooder.

Gill rakers are moderately short and slender, with 9 or 10 rakers in the outer row on the lower part of the first gill arch.

Contained species

Chetia flaviventris Trewavas, 1961 (Type species). Tributaries of the Limpopo and Incomati rivers, Transvaal, South Africa.

Diagnosis and discussion

The single species in this genus is distinguished from the other fluviatile '*Haplochromis*'-group species, except *Serranochromis*, by the nature of the anal fin markings in adult males, which are numerous, small and non-ocellate (and which barely differ from those in females). In addition, *Chetia* is distinguished from *Ctenochromis*, *Orthochromis* and *Thoracochromis* by the nature of the scale pattern in the thoracic–abdominal region (a gradual as compared with an abrupt size change in the scales of the two body regions).

From *Serranochromis*, *Chetia* is distinguished mainly by having fewer (14 or 15) abdominal vertebrae (cf. 16–18, rarely 15, in *Serranochromis*) and by having bicuspid teeth in specimens of a larger size. In meristic characters, other than vertebral numbers, the two genera have a comparable overlap, but for each feature the modal values are distinct, those for *Serranochromis* being the higher.

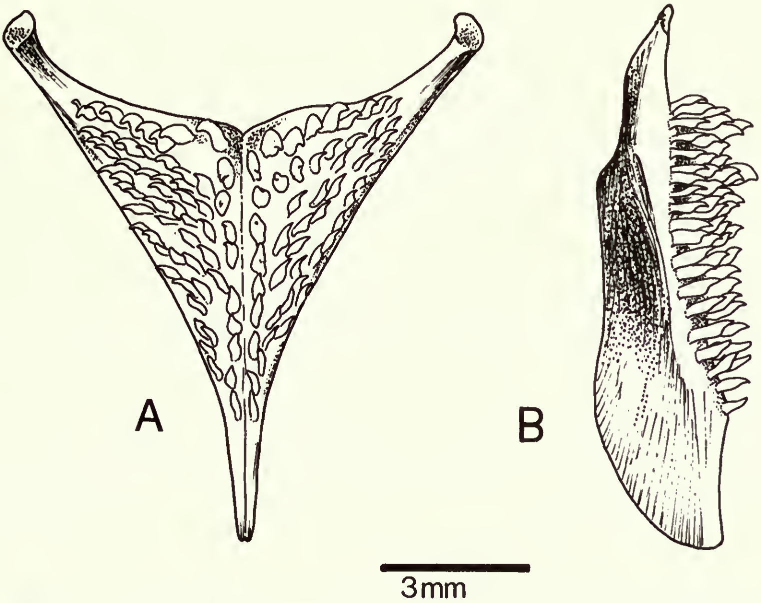

Fig. 19 Lower pharyngeal bone of *Chetia flaviventris*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

I can detect no apomorph features which would suggest that *Chetia* might be related to any of the three lineages showing an abrupt size change in the thoracic–abdominal squamation, and nor can I find apomorph characters to associate it with *Haplochromis*, *Astatotilapia* or *Astatoreochromis*.

That *Chetia* and *Serranochromis* share a similar kind of anal fin marking does not necessarily imply a close relationship between them either, since it seems likely that this is a primitive (plesimorph) feature for '*Haplochromis*'-group species (see above, p. 275). I can detect no unequivocally synapomorphic features common to *Chetia* and *Serranochromis* and thus, despite their superficial similarities, cannot place the taxa in the same genus.

Likewise, the almost identical anal fin markings in *Chetia* and '*Haplochromis*' *darlingi* (see below, p. 310) cannot be taken to indicate a close relationship. It is for this reason, as well as their lack of uniquely shared apomorph features and the presence of autapomorph features in each species, that has led me to place *Chetia flaviventris* and '*H.*' *darlingi* in separate lineages, and thus to give the latter taxon generic rank (see p. 312).

Trewavas (1964 : 10) has remarked on the similarity between *Chetia* and certain *Serranochromis* species, a similarity which led her to consider *Chetia* an offshoot from a lineage that also contains *S.* (*Serranochromis*) *thumbergi* and *S.* (*S.*) *robustus*. That there are similarities between the three species is undeniable, but *Chetia* does not share with the two *Serranochromis* species (and with other species of the genus) the derived feature of a high number of abdominal vertebrae. It does, of course, share with all *Serranochromis* (*Serranochromis*) species the early ontogenetic appearance of unicuspid outer and inner jaw teeth (see p. 300), an apomorph feature which *Serranochromis* (*Sargochromis*) does not share with the nominate subgenus.

Thus at present, one cannot find a totality of shared apomorph features which would indicate a clear-cut sister group relationship for *Chetia*. For that reason I would consider that *Chetia* is best represented as a monotypic lineage (genus) of uncertain affinities. Intuitively one suspects that *Chetia* is related either to *Serranochromis* (especially the nominate subgenus of that taxon) or to '*Haplochromis*' *darlingi*. But, the evidence to propose formally one or other of these relationships is not available if the classification adopted is to reflect phyletic relationships.

Superficially, *Chetia* also resembles one of the Angolan '*Haplochromis*' species, '*H.*' *welwitschii* Blgr., a taxon known only from its now poorly preserved holotype. Until more and better documented material of the Angolan '*Haplochromis*' is available for study, any possible relationship between *Chetia flaviventris* and '*H.*' *welwitschii* cannot be investigated (see also p. 312 below).

PHARYNGOCHROMIS gen. nov.

TYPE SPECIES. *Pelmatochromis darlingi* Blgr., 1911. (Holotype in the BMNH collections.)

SYNONYMY. See Regan (1922*a*).

Description

Body form moderately slender (body depth 30–33% of standard length).

Squamation. The body squamation type and pattern is like that in *Chetia* (see p. 307). The cheek is fully covered by 4 or 5 horizontal scale rows. There are 32–34 (modes 32 and 33), rarely 31, scales in the lateral line.

Neurocranium. The preotic portion of the skull is slightly less protracted that in *Chetia*, the brain case is a little higher and the slope of the dorsal skull profile a little steeper. In other words, the overall skull morphology is somewhat more like that in *Serranochromis* (*Sargochromis*) species than in *Chetia*, a resemblance that may be associated functionally with the enlarged pharyngeal bones and dentition present in both taxa.

Vertebral numbers: 29 or 30 (mode 29), comprising 13 or 14 (mode 14) abdominal and 15 or 16 (mode 15) caudal elements. An apophysis for the dorsal retractor pharyngeal muscles is present on the third centrum.

Dentition. There is a predominance of unicuspid, caniniform teeth in the outer row of both jaws in fishes over 60 mm standard length, but even in the largest specimens examined (90 mm SL) many unequally bicuspid teeth persist (and, occasionally, may be the predominant form). Unicuspids also predominate in the inner tooth rows, the other teeth being bi- or weakly bicuspid.

The inner rows of both jaws are arranged in two series anteromedially and a single row laterally and posteriorly.

Jaws. The lower jaw is somewhat shorter and deeper than in *Chetia*, but the premaxilla is similar in both genera.

Lower pharyngeal bone and dentition. The dentigerous surface is equilateral or almost so, and the bone itself is somewhat thickened medially (noticeably so when compared with that in *Chetia*). The two median tooth rows are composed of coarse, stout and molariform or submolariform teeth (Fig. 20), the latter retaining traces of a small, near-central point on the occlusal surface. The teeth in the row, or the two rows on either side of the median series, are markedly coarser than those in the lateral rows (which are also clearly cuspidate), and may have submolariform crowns.

Dorsal fin with 14 or 15 (mode 14), rarely 13, spines and 10–12 (mode 11) branched rays.

Anal fin with 3 spines and 7–8 branched rays.

Caudal fin skeleton. All hypurals are free in the 4 specimens (including the holotype) radiographed.

Caudal fin: strongly truncate to virtually rounded.

Pelvic fin: with the first branched ray the longest.

Anal fin markings in male fishes. As in *Chetia* and *Serranochromis*, there are numerous (up to 18, according to Bell-Cross, 1976), small orange spots on the soft part of the fin, and sometimes extending onto the membrane between the spines as well. *Pharyngochromis darlingi* is a female mouthbrooder (Bell-Cross, 1976). For coloured illustrations see Jubb (1967*a* : pl. 46); Bell-Cross (1976 : pl. 16).

Gill rakers are short and stout, with 9 or 10 (less commonly 7 or 8) in the outer row on the lower part of the first gill arch.

Contained species

Pharyngochromis darlingi (Blgr.), 1911. Type species. Widely distributed in the Zambesi river system and southwards to the Limpopo.

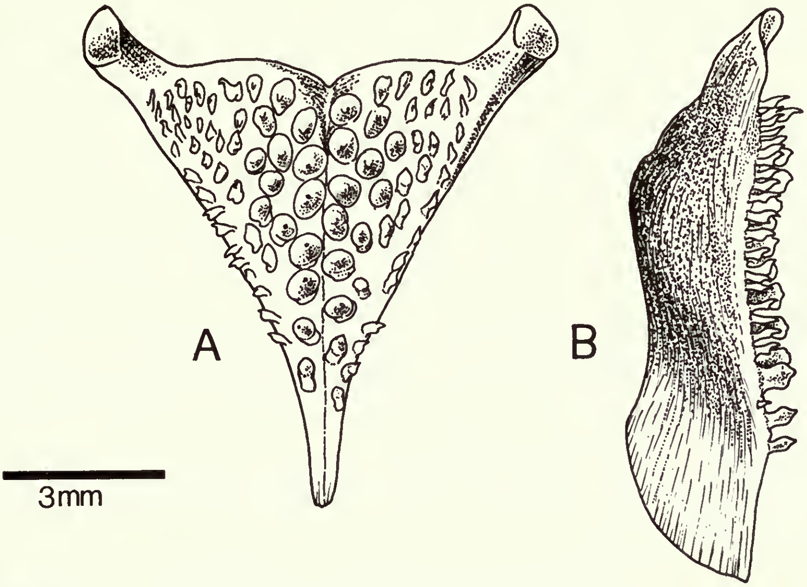

Fig. 20 Lower pharyngeal bone of *Pharyngochromis darlingi*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

Poll (1967) recorded this species (as *Haplochromis darlingi*) from Lake Calundo (Zambesi drainage), Angola, and also redetermined, as *H. darlingi*, specimens from the Cubango river which Pellegrin (1936) had identified as *Haplochromis welwitschii*. However, judging from the nature of the anal fin markings in male specimens, I suspect that these specimens should not be referred to *P. darlingi*. Their identity should be more firmly established (possibly as a yet undescribed species) when a thorough revision of the Angolan '*Haplochromis*' species is carried out (see p. 312).

The same features distinguishing *Chetia* from the other fluviatile '*Haplochromis*'-group genera, including *Serranochromis*, also serve to distinguish *Pharyngochromis*.

From *Chetia* itself, *Pharyngochromis* is distinguished, chiefly, by its stouter lower pharyngeal bone and its partly molarized dentition, by having lower modal numbers of abdominal and caudal vertebrae, fewer lateral line scales, and by having a larger proportion of bicuspid teeth in the outer tooth row of both jaws in fishes more than 40 mm standard length.

My reason for not treating *Chetia flaviventris* and *Pharyngochromis darlingi* as members of the same genus is their lack of shared derived features (see above, p. 310). The same reasons led me to exclude *Pharyngochromis* from the *Sargochromis* division of the *Serranochromis* lineage.

Presumably it is the presence of enlarged pharyngeal teeth, as well as overall similarity in body form and oral dentition, that led Trewavas (1964 : fig. 1 and p. 9) to place *P. darlingi* at the base of a lineage leading to *Sargochromis* (then restricted to the type species, *S. codringtoni*). Derivatives from, and members of, this lineage also included a number of Zambesi '*Haplochromis*' species which I now place in *Sargochromis*.

Since the subgenera *Serranochromis* and *Sargochromis* share certain derived features (especially an increased number of abdominal vertebrae) not found in *Pharyngochromis* it would seem more parsimonious to consider that the two former taxa share a recent common ancestry and that any relationship they may have with *Pharyngochromis* is a more distant one.

The alternative classification implicit in Trewavas' (1964) phyletic diagram, that *Chetia* and *Serranochromis* (i.e. my subgenus *Serranochromis* (*Serranochromis*)) are sister-groups, and that *Sargochromis* (i.e. my subgenus *Serranochromis* (*Sargochromis*)) plus *Pharyngochromis* is the sister-group of *Chetia* and *Serranochromis* combined, is not supported by the distribution of derived characters amongst the taxa involved. Such an arrangement would also imply that the derived features shared by *Sargochromis* and *Serranochromis* were evolved independently. Admittedly in my scheme one specialized feature (the enlarged pharyngeal bones and dentition of *Pharyngochromis* and most *Sargochromis* species) would have to be evolved independently. But, evidence from haplochromine lineages in Lake Victoria (see Greenwood, 1974*a*) and from *Thoracochromis* (e.g. *Th. mahagiensis* and *Th. pharyngalis*) seems to indicate that the independent evolution of an enlarged pharyngeal mill is not uncommon amongst '*Haplochromis*'-group cichlids.

To summarize: the relationships amongst those '*Haplochromis*'-group taxa with non-ocellate and numerous anal fin spots (a group essentially of the Zambesi, Limpopo, and Angolan rivers) cannot clearly be recognized at present. Two lineages with a presumed recent common ancestry (*Serranochromis* and *Sargochromis*) are treated as sister-groups and given subgeneric rank; the other two lineages cannot be related unequivocally (on the basis of shared derived characters) with either the *Serranochromis–Sargochromis* lineages or with one another; each therefore is treated as a monotypic and monophyletic assemblage (on the basis of autapomorphic features) and given generic rank (*Chetia* and *Pharyngochromis*).

The further resolution of relationships amongst these taxa awaits more detailed studies of their contained species (and of the Angolan '*Haplochromis*' species), and an understanding of the phyletic importance which can be attached to anal fin markings.

The Angolan '*Haplochromis*' species

Several references have been made to these little-known and poorly represented taxa. The last comprehensive revision of the Angolan *Haplochromis* was that of Regan (1922*a*) who recognized three species, *H. humilis* (Steindachner), 1866, *H. acuticeps* (Steindachner) 1866 and *H. multiocellatus* (Blgr.) 1913. For some reason not stated (but probably because Boulenger (1915) included both species in *Pelmatochromis*), Regan omitted Steindachner's (1865) *Hemichromis angolensis* and Boulenger's (1898) *Pelmatochromis welwitschii*. Both species, however, would have fallen into Regan's definition of *Haplochromis*.

All the specimens representing these species (and others synonymized therein by Regan, 1922*a*) are poorly preserved, mostly represented by a single individual (or at best 4 or 5 syntypes), and often without precise locality data; the type of *P. angolensis* is now lost (see Bell-Cross, 1975 : 427).

In recent years Poll (1967) has added three species (*H. thysi*, *H. machadoi* and *H. schwetzi*; see pp. 305 and 297 above for the first two species respectively), Trewavas and Thys van den Audenaerde (1964) a fourth (*H. albolabris*) and Penrith (1970) a fifth (*H. buysi*).

My revision of this material indicates that probably several lineages are represented within it, and that Regan's (1922*a*) re-definition of *H. acuticeps* (Steindachner) embraces at least two species. Some of the Angolan species seem to show affinity with the genus *Astatotilapia*, others with *Chetia* and some may represent lineages yet unrecognized. But, until the species can be revised and reviewed on the basis of more extensive, better preserved and better documented collections I believe that it is inadvisable to place any species in the genera recognized in this paper. It is certainly impossible to demonstrate that the Angolan species are more closely related to one another than to any other lineage, although intuitively one recognizes, in at least some species, an 'Angolan facies' and feels that this overall appearance suggests relationships with the Zambesi–Limpopo genera.

Trewavas' (1964) phyletic diagram illustrating the possible relationships of '*Serranochromis*' and '*Sargochromis*' indicates that a number of Angolan '*Haplochromis*' species are related to '*Serranochromis*' (i.e. the subgenus *Serranochromis* (*Serranochromis*) as defined on p. 299). I can find no synapomorph characters to support this supposition. The very faint traces of anal fin markings left on the holotype of *H. welwitschii* suggest that they may be of the *Serranchromis–Chetia–Pharyngochromis* pattern but this is probably a plesiomorph feature. Where anal fin markings are detectable in the other species mentioned by Trewavas (1964), for example *H. lucullae*, they appear to be of the true ocellar type and thus a derived feature not represented in *Serranochromis*.

The number of vertebrae (especially the abdominal elements) in *H. welwitschii* and the other Angolan species is lower than that in *Serranochromis* (although within the range for *Chetia*) and again represents a plesiomorph condition.

Other characters and character states are equally lacking in shared apomorph features, or represent autapomorphies characterizing the Angolan taxa alone.

As a temporary expedient I can only suggest that the Angolan species be given no formal generic status and that they should be referred to under the informal epithet '*Haplochromis*', whose use in no way implies a close relationship with the species of *Haplochromis* (or, indeed, the majority of species previously referred to that genus).

Summary and conclusions

I am well aware of the shortcomings in this preliminary attempt to clarify the phylogenetic relationships of '*Haplochromis*'-group cichlids, and in particular members of that manifestly polyphyletic 'genus' *Haplochromis*.

Two major difficulties were encountered, and although one has been overcome to a greater or lesser degree, the other still stands in the way of a fully phylogenetic classification. The first difficulty lies in determining morphocline polarity amongst the characters available for research of this kind (p. 270). Then, when plesiomorph and apomorph features are recognized, there is the problem caused by an apparent absence of synapomorphic features at the various levels of relationship necessary to construct a truly cladistic classification.

In other words, one can identify fairly readily what appear to be monophyletic lineages, but the difficulties arise when one attempts to interrelate the different lineages on a sister-group basis.

The problem is well exemplified by the genera *Ctenochromis*, *Thoracochromis* and *Orthochromis*. All three taxa share the presumably derived feature of an abrupt size-change between the scales on the thoracic and ventrolateral flank regions of the body (see p. 270), and thus are assumed to share, at some level, a common ancestry. Both *Orthochromis* and *Ctenochromis*, but not *Thoracochromis* exhibit derived features that are unique for each genus (i.e. autapomorphies) but there are no synapomorphic characters that would indicate which two of the three genera are more closely related to one another. Since *Thoracochromis* shows only one apomorph feature common to all its species it is, presumably, the least derived member of the trio.

Similar difficulties arise with *Haplochromis*, *Astatotilapia* and *Astatoreochromis*, taxa which appear to be interrelated (along with the components of the Victoria–Edward–Kivu species flock) only on the basis of their possessing true ocellar spots on the anal fin of male fishes (p. 274). *Haplochromis* and *Astatoreochromis* (and each of the major lineages in the Victoria flock) have clear-cut autapomorphic features; *Astatotilapia*, apparently, has none. Again one is left with an unresolved polychotomy, but in this case, because the lake flocks are involved, a far more complex one.

Finally, but in a rather different category, since no unifying synapomorphic characters have been detected, are the genera *Chetia*, *Pharyngochromis* and *Serranochromis*. Intuitively the taxa would seem to be interrelated (as they have been assumed to be by other workers, e.g. Trewavas, 1964), probably because of their similar overall morphology, coloration, and the repeated occurrence of enlarged pharyngeal mills amongst their constituent species; in addition, the species form a well-defined, Zambesian geographical group. Yet, I have failed to substantiate their presumed relationship because there are no apparently derived features common to all three genera (see p. 312). Of course, my interpretation of one shared feature (the non-ocellate, and very numerous anal spots) as a primitive condition may be incorrect (see p. 275); only further research, especially comparative ethological research, can clarify that point.

Further research is also needed to test the phylogenetic homogeneity of the speciose lineage *Thoracochromis* (see above and p. 294). As yet no way has been found to test the possibility, indicated by certain morphological features, that there are three infragroups represented in the lineage, viz. one in Lake Turkana, another in the Nile and Lake Albert (including also the outlier species from Lake Edward and possibly Lake Victoria), and a third from the Zaire river system.

Despite these limitations I believe that the classification suggested here is a more efficient one than that existing at present (the term 'efficient' used *sensu* Patterson & Rosen (1977 : 158–159) to denote a classification from which a '. . . theory of relationships is recoverable . . . without loss of information'). Clearly its efficiency can be improved, but that must await the phyletic analysis of '*Haplochromis*'-group species in the Great Lakes, especially those of Lakes Malawi and Victoria.

It has been generally assumed (see Regan 1921*b*; Trewavas, 1935; Fryer & Iles, 1972) that the Malawi '*Haplochromis*'-group species were derived from an anatomically generalized fluviatile '*Haplochromis*' (i.e. *Astatotilapia*) species. I now suspect, however, that the story is far more complex, that the Malawi flock is probably of polyphyletic origin and that lineages related to *Thoracochromis* as well as to *Astatotilapia* and even to *Serranochromis* and *Chetia* may have contributed to the flock. Possibly some of the ideas put forward in this paper may contribute to the elucidation of that problem.

Likewise the assumed monophyly of the Lake Victoria '*Haplochromis*' species flock (Greenwood, 1974*a*) must be thrown into doubt, because no characters have been found to support this concept (see p. 269). As compared with Lake Malawi, however, it does seem more likely that fewer and phyletically more closely related lineages were involved, and that most are related to the *Astatotilapia* lineage.

Geographically, the different lineages dealt with in this paper have interesting patterns of distribution.

Thoracochromis is essentially a Nilotic–Zairean taxon (see p. 294). Unlike the others with Zairean representatives (see below), it is best represented in the lower reaches of that river, since only one species (*Th. moeruensis*) is recorded from the upper Zaire system (see p. 293).

The virtual absence of *Thoracochromis* from Lakes Victoria, Edward and Kivu is, on the basis of its overall distribution, rather surprising. Possibly this is attributable to the relatively recent association between these lakes and the Nile system (see Beadle, 1974 : 139–146; Greenwood, 1974*b* and 1976; Berry, 1976; Livingstone, 1976; Rzóska, 1976*a* & *b* : 2–29). Lake Turkana and, as far as can be told, Lake Albert as well, have only ever had major and direct interconnections with the Nile system; the geologically recent riverine connection between Lakes Albert and Victoria probably is made impassable to fishes by the presence of the Murchison Falls (now Kabalega Falls), and the connection between Lakes Edward and Albert via the Semliki river also seems to be impassable for most fishes (see discussions in Greenwood, 1959*b*, 1973 and 1976; also Rzóska, 1976*c* : 197–202).

Astatotilapia, apart from its outliers in North Africa (*A. desfontainesi*), Syria and Israel (*A. flaviijosephi*) and possibly in Nigeria (see p. 283), is essentially a lineage of the eastern Rift Valley (except Lake Turkana) and the rivers of eastern Africa; it is represented in the Zaire drainage only by its species in Lake Tanganyika (see p. 284). The absence of *Astatotilapia* from Lake Turkana probably is to be explained through the history of that lake (see above). Far more puzzling is the occurrence of two *Astatotilapia* species north of the Sahara (Tunisia, Algeria, Syria and Israel), and the possibility of one or two other species in Nigeria. This disjunct distribution may, of course, be the result of incorrectly assessing the phyletic relationships of the outlier species. On currently available evidence, however, there is nothing to suggest how else these outlier species might be interrelated.

Ctenochromis, with one exceptional species (*C. pectoralis*) from southeastern Tanzania (Indian Ocean drainage), is totally Zairean (including Lake Tanganyika) in its distribution (see p. 289). *Orthochromis* too is an essentially Zairean lineage and, like *Ctenochromis*, is confined to the upper parts of that system; it has a representative in the Malagarasi river system of Tanzania, but historically that river should be considered part of the upper Zaire drainage (Poll, 1956). The only outlier species, *Orthochromis machadoi*, occurs in the Cunene river, Angola, a river whose ichthyofaunal affinities are closer to those of the Zambesi than the Zaire (Poll, 1967).

Serranochromis is widely distributed (see p. 302), having representatives in the Zaire and Zambesi systems, as well as in the Limpopo and certain Angolan rivers (including the Cunene). Both its Zairean and Zambesi components are confined to the upper portions of their respective systems (cf. the distribution of *Thoracochromis*).

Chetia and *Pharyngochromis* have, geographically speaking, the most restricted distributions of all the fluviatile species considered in this paper (apart from *Astatoreochromis* which occurs only in parts of the Malagarasi and Lukuga rivers, in Lakes Edward and Victoria and in some physiographically related water bodies, see p. 286). *Chetia*, a monotypic genus, is confined to the Limpopo drainage system, and *Pharyngochromis*, also monotypic, to the Upper and Middle Zambesi, the Sabi–Lundi system and the Limpopo system.

The only truly lacustrine lineage discussed in this paper, *Haplochromis*, is confined to Lakes Victoria, Edward, George and Kivu. The significance of this distribution, and the possible relationships of the genus, will be discussed in a forthcoming revision of the lineages from those lakes.

Key to the genera

Notes (i) When citing the range for meristic characters, values rarely encountered are given in square brackets and precede or follow, respectively, the most frequently recorded low and high values for that character.

(ii) Modal values (or modal ranges) are in bold type and enclosed in round brackets.

(iii) Gill raker counts are for the outer row of rakers on the lower part of the arch, and do not include the raker (if such is present) on the epi-ceratobranchial articulation.

(iv) For further notes, and definitions of the characters used see pp. 270–276.

Key

A gradual change in size between the scales on the chest (i.e. ventral and ventrolateral body region anterior to the insertions of the pectoral and pelvic fin bases) and those on the ventral and ventrolateral aspects of the flanks and belly (see Fig. 1) 1

An abrupt size change between the small scales on the chest and the larger scales on the ventrolateral and ventral aspects of the body, the size demarcation line usually running between the pectoral and pelvic bases (but sometimes a little before or behind that level; see Figs 2, 3 & 9) . . . . 2 (p. 316)

1) (a) Anal fin in adult males with 3–9 (**3** or **4**) ocelli (coloured spots each with a clear or translucent area surrounding it) arranged in one or two lines and lying about midway between the base and the distal margin of that fin. (Most females and juvenile males with 3 or 4 non-ocellate spots in the same position, or fin without spots.) Scales below (and often those above) the upper lateral line ctenoid, the ctenii arranged along almost the entire free margin of the scale. Anal fin with 3 spines (individuals with 4 spines are so rare that this number can be considered as an individual abnormality). Dorsal fin rarely with more than 16 spines. Marked sexual dimorphism in adult coloration (males colorful, females drab) . . . . A

(b) Anal fin in adult males with 6–20 ocelli arranged in 3–5 regular rows and thus occupying a large area on the soft part of the fin; females with a similar pattern if spots (non-ocellate) are present. Anal fin with 3–6 spines, dorsal fin with 16–20 (**17–19**) spines. Caudal fin rounded. Lower pharyngeal bone thickened (strongly so in two species), its dentition partially or completely molarized. No marked sexual dimorphism in coloration; body colour yellow–green, fins with a maroon flush. Other features as in 1(a) above *Astatoreochromis* (p. 285)

(c) Anal fin in both sexes with numerous (18–40) small spots, none with a clear or translucent surround, not arranged in regular rows but covering most of the area of the soft anal fin; similar spots on the soft dorsal and the caudal fins. Scales below the upper lateral line are cycloid or predominantly cycloid; when ctenoid scales are present the ctenii are weak and confined to a small median sector on the free margin of the scale. . . . B

A) (i) Jaw teeth in the outer row (and sometimes the inner rows as well) with obliquely cuspidate compressed crowns, the major cusp drawn out beyond the tooth's vertical axis (see Fig. 7), the minor cusp reduced or absent. 12–14 (**13**) abdominal and 15 or 16 caudal vertebrae (total 28–30; **28** and **29**). Dorsal fin with 14–16 (**15** and **16**) spines and 8–10 (**9**) branched rays. Anal fin with 3 spines and 7–10 (**9**) branched rays. Lateral line with 29–34 (**30–32**) scales. Cheek with 3 [4] horizontal rows of scales. Caudal fin truncate or weakly subtruncate. Lower pharyngeal bone without any noticeably enlarged or coarse teeth in the two median rows. Gill rakers [7] 8–10 (**9**) . . . . ***Haplochromis*** (p. 278)

(ii) Jaw teeth in the outer row unequally bicuspid or unicuspid, the crown neither compressed nor obliquely truncate, its tip lying within the tooth's vertical axis (see Fig. 4). Outer teeth mostly bicuspids in fishes <70 mm SL; an admixture of bi- and unicuspids in larger fishes, with unicuspids predominating in specimens >100 mm SL. Inner teeth predominantly tricuspid, small. 12–14 (**13**) abdominal and 14–16 (**15**) caudal vertebrae (total 27–30; **28** and **29**). Dorsal fin with 14–16 (**15**) spines and 8–11 (**9** and **10**) branched rays. Lateral line with 28–30 (in one species 31–34) scales, cheek with [2], **3**, [4] horizontal rows of scales. Caudal fin rounded or slightly subtruncate. Lower pharyngeal bone with at least the two median rows composed of coarser (sometimes molariform) teeth. Gill rakers [7] 8 or 9 . ***Astatotilapia*** (p. 281)

B) (i) Abdominal vertebrae 13 or 14 (**14**), caudal vertebrae 15 or 16 (**15**), total number of vertebrae 29 or 30 (**29**). Dorsal fin with 14 or 15 (**14**) spines and 10–12 (**11**) branched rays. Lateral line with 32–34 (**32** and **33**) scales, cheek with 4 or 5 horizontal rows. Outer row of jaw teeth composed of unequally bicuspids in fishes <60 mm SL, unicuspids present and becoming commoner in larger individuals. Lower pharyngeal bone thickened, at least the two median rows composed of enlarged and molariform teeth (see Fig. 20). Gill rakers [7 or 8] **9** or **10**. Anal fin with up to 20 spots . . . . ***Pharyngochromis*** (p. 310)

(ii) Abdominal vertebrae 14 or 15, caudal 15–17 (**16** and **17**), total number of vertebrae 30–32 (**31**). Dorsal fin with 14 or 15 spines and 11 or 12 branched rays. Lateral line with 34 or 35 scales, cheek with 5 or 6 horizontal rows of scales. Outer row of jaw teeth mainly unicuspids in fishes >30 mm SL, some weakly bicuspids (the minor cusp a shoulder rather than a point) present in smaller individuals. Lower pharyngeal bone not thickened, without molariform or submolariform teeth (see Fig. 19). Gill rakers 9 or 10 . . . . ***Chetia*** (p. 307)

(iii) Abdominal vertebrae [15] 16–18 [19] (**16** and **17**), caudal vertebrae 12–16 (**14** and **15**), total number of vertebrae 28–32 (**31**). Dorsal fin with 13–16 (**15** and **16**) spines and 11–16 (**12** and **13**) branched rays. Lateral line with 28–34 (**30** and **31**) scales, cheek with 3–6 (**3** – **5**) horizontal rows of scales. Outer jaw teeth mostly unequally bicuspids in fishes <150 mm SL, predominantly unicuspids in larger individuals. Lower pharyngeal bone thickened in all but one species, and in all but that species with at least the two median tooth rows composed of enlarged and molariform teeth (see Fig. 18); the exceptional species has coarse and slightly enlarged, but cuspidate, teeth in the median rows (see Fig. 18A), Gill rakers 9–15 (**12** and **13**). Anal fin with up to 40 spots. . . . . ***Serranochromis*** (***Sargochromis***); p. 303)

(iv) Abdominal vertebrae [15] 16–18 [19] (**16** and **17**), caudal vertebrae [15] 16–18 (**16** and **17**), total number of vertebrae 31–36. Dorsal fin with 13–18 (**15** and **16**) spines and 13–16 (**14–16**) branched rays. Lateral line with [34] 35–41 scales, cheek with 3–11 (**5–9**) horizontal rows of scales. Outer jaw teeth predominantly or entirely unicuspids in fishes >30 mm SL. Lower pharyngeal bone not thickened, either elongate and narrow (see Fig. 14A & B) or its dentigerous surface almost equilateral in outline (see Fig. 14C); no teeth molariform, even the median row teeth only slightly coarser than the others. Gill rakers [8] 9–13 (**10–12**). Anal fin with up to 40 spots ***Serranochromis*** (***Serranochromis***); p. 299)

2) (a) Pelvic fin with the first branched ray the longest. Scales on ventral body surface behind pelvic fins not markedly reduced in size (see Fig. 9) 2A

(b) Pelvic fin with the second or third branched ray the longest. Scales on ventral body surface and on ventrolateral aspects of flanks small to minute (see Fig. 3). Cheek naked or, if scaled, with a definite naked area along its entire ventral (preopercular) margin. Chest completely scaled, or partly scaled, or naked. Dorsal fin with 16–20 (**17** and **18**) spines and 9–11 (**9** or **10**) branched rays. Anal fin with 3 or 4 spines and 7–10 branched rays. Lateral line with 30–35 (**30** and **31**) scales. Head profile strongly decurved, eyes suprolateral in most species . . . . ***Orthochromis*** (p. 295)

2A) (i) Chest with a naked patch or extensive naked area on each side of the body (see Fig. 9). At least the ventral part of the cheek scaleless (almost the entire cheek naked in one species). Anal fin with 3 spines and 6–9 (**6–8**) branched rays. Lateral line with 27–33 (**28** and **30** or **31**) scales . . . . ***Ctenochromis*** (p. 287)

(ii) Chest completely scaled. Cheek completely or almost completely scaled (i.e. one horizontal row absent ventrally). Dorsal fin with 13–16 [17] (**14–16**) spines and 8–10 [11] (**9** and **10**) branched rays. Anal fin with 3 spines and 6–10 (**7–9**) branched rays. Lateral line with 29–32 (**30–32**) scales . . . ***Thoracochromis*** (p. 290)

Appendix 1

A replacement 'generic' name for the Lake Malawi '*Haplochromis*' species

Since the genus *Haplochromis* is now restricted to five species, all members of the Lakes Victoria, Edward, George and Kivu species flock (p. 280), the Lake Malawi species formerly referred to *Haplochromis* are without a generic name. Because it is obvious that the '*Haplochromis*' of Lake Malawi are a polyphyletic group, any generic placement at the present time must be considered merely a formal nomeclatural action unrelated to the phyletic affinities of the species.

Two generic names would appear to be available for this purpose (see Trewavas, 1935), namely *Cyrtocara* Boulenger (1902) and *Champsochromis* Boulenger (1915). A third name, *Otopharynx*, Regan (1920), apparently is also available, but it is junior to the others and there are anatomical grounds for regarding its contained species as representing a lineage distinct from that to which many Malawi '*Haplochromis*' belong (Greenwood, 1978).

Cyrtocara (type species *C. moori*) has a pharyngeal apophysis of the typical '*Haplochromis*'-type (Trewavas, 1935) and its oral dentition is composed of slender unicuspid outer teeth and mixed uni- and tricuspid inner teeth.

Although at least some members of the type species have a moderately developed hump in the frontal region of the head, I can see no morphological grounds for not accepting *Cyrtocara* as a temporary formal name for the '*Haplochromis*' species of Lake Malawi. I thus propose that it be used in that capacity until the Malawi species are revised. This action by no means implies that I consider many of these species to have a true phyletic relationship with *Cyrtocara moori*.

Appendix 2

The taxonomic status of the genus *Limnotilapia* Regan, 1920

In a recent paper (Greenwood, 1978) I treated the genus *Limnotilapia* Regan (1920) as a synonym of *Simochromis* Boulenger, 1898, thus unintentionally anticipating the publication of a paper giving detailed reasons for this nomenclatural change. Since publication of the paper in which the two 'genera' are to be discussed is likely to be delayed further, the reasons for synonymizing *Limnotilapia* with *Simochromis* are dealt with below.

A comparison of Regan's (1920) description for *Limnotilapia* with his redescription of *Simochromis* reveals that the taxa apparently are differentiable only on the former having a rather small, terminal mouth, and the latter having the mouth subterminal and rather wide.

When the type species of the genera, *Limnotilapia dardennii* (Blgr.) and *Simochromis diagramma* (Günth.), are compared, these differences can be translated into more substantial osteological ones involving the morphology of the premaxilla and dentary.

Viewed from below (i.e. occlusally), the premaxillary outline in *L. dardennii* is gently curved and relatively narrow; in other words, it has an outline approximating to that of a Norman arch. The premaxillary outline in *S. diagramma*, by contrast, has a virtually straight and wide anterior margin, with the short posterior dentigerous arms meeting it almost at right angles; the outline of the bone is thus more nearly that of a hollow square. The posterior dentigerous arms of the premaxilla in *S. diagramma* are slightly bullate, whereas in *L. dardennii* they are slender and compressed.

There are, of course, comparable interspecific differences in the occlusal outline of the dentary. In *Limnotilapia dardennii* the lateral arms of the dentary are protracted relative to the transversely directed anterior part of the bone, and the outline of the whole bone is similar to that of the premaxilla. In *Simochromis diagramma* the dentary, like the premaxilla, is foreshortened, with the short lateral dentigerous arms (about equal in length to the transverse part) meeting the slightly curved transverse portion at almost a right angle. The dentary in *S. diagramma* also differs from that of *L. dardennii* in having virtually no upward sweep to its coronoid portion; in *L. dardennii* this region slopes upward at a gentle but noticeable angle.

Seen in these terms, the osteological 'morphological gap' separating the taxa would appear to be a more substantial one than that expressed in Regan's (1920) key and generic synopsis. But, the 'gap' is bridged when one examines the premaxilla and dentary of *Limnotilapia loocki* Poll, 1949 (see Poll, 1956 : 62, fig. 10 for an expanded description of the species, and illustrations of the jaws and dentition).

The morphology of both these bones in *L. loocki* is virtually intermediate between those in *L. dardennii* and *S. diagramma*. Thus, it is impossible to differentiate the 'genera' on the osteological features characterizing the jaws of the type species. Furthermore, the external oral characters used by Regan (1920) also intergrade when growth-series of the type species are examined, and I have been unable to detect other characters that might serve to distinguish the taxa (it being understood that the 'genera' are being interpreted here, as they were by Regan, merely on the presence of a discrete morphological gap that is 'greater' than one which might be used to characterize species). There would, therefore, seem to be no grounds for treating *Limnotilapia* and *Simochromis* as distinct genera, the more so when one considers the various (and apparently synapomorphic) features that are shared by all but one of their included species.

Limnotilapia loocki (like *L. dardennii*, *Simochromis diagramma*, *S. babaulti* Pellegrin, *S. curvifrons* Poll and *S. marginatus* Poll) has, in both jaws, slender-shafted, recurved, outer teeth with markedly compressed and expanded, obliquely bicuspid crowns, a greatly reduced (or absent) interspace between the numerous inner and single outer tooth rows in both jaws, a densely toothed lower pharyngeal bone (the teeth fine and compressed) and a strongly decurved anterior profile to the neurocranium (where, in some species, the ethmovomerine region is almost vertically inclined) In all these species, too, the chest scales are small, deeply embedded and have an abrupt size demarcation with the larger scales on the anterior abdominal region of the body.

For the moment it is these apparently apomorphic features which should be used to define the genus *Simochromis* Blgr., 1898 (with which is now included, as a junior synonym, the genus *Limnotilapia* Regan, 1920).

The one species not included in the character analysis given above is *Limnotilapia trematocephala* (Blgr., 1901), a taxon known only from its holotype. I have not, of course, been able to examine all the relevant osteological features in this specimen, but its relatively sparsely toothed lower pharyngeal bone, the morphology of its outer row jaw teeth (which are without noticeably compressed, expanded and obliquely bicuspid crowns, and which are not strongly recurved), and its relatively large pectoral scales, all suggest that the species probably belongs to a different lineage and should not, therefore, be included in the genus *Simochromis*.

For the moment it is impossible to indicate the phyletic relationships of the genus *Simochromis*, either within or without the cichlid flocks of Lake Tanganyika. Much further research will be required before this can be achieved (and will also be needed before a generic placement of '*Limnotilapia*' *trematocephala* can be effected).

As was noted in my paper on the pharyngeal apophysis in African cichlids (Greenwood, 1978), *Simochromis dardennii* has a near-typical *Tilapia*-type of apophyseal structure. *Simochromis loocki*, on the other hand, has an apophysis of the modified *Tropheus*-type; the basioccipital is inflated and bullate, with its ventral tip almost reaching the level of the parasphenoidal facets but not contributing in any way to the articular surface provided by these facets. In its general organization, the apophysis in *S. loocki* is intermediate between the *Tilapia* and *Tropheus* types (see Greenwood, 1978), but differs from the modal condition of both types in having the basioccipital noticeably inflated.

Since *S. dardennii* (with a *Tilapia*-type apophysis) has the least specialized premaxillary and dentary of any *Simochromis* species, and since *S. babaulti* and *S. diagramma* have the most derived jaws (the species having, respectively, *Tropheus* and near *Haplochromis* type apophyses; see Greenwood, 1978), it is tempting to conclude that in this lineage the *Tilapia*-type apophysis is the plesiomorph one. That *S. loocki* (whose jaw morphology is intermediate between that of *S. dardennii* and those of the other *Simochromis* species) has an apophysis intermediate between the *Tilapia* and *Tropheus* types, would also seem to support this hypothesis.

Acknowledgements

I am deeply indebted to my colleague, Gordon Howes, for all the assistance he has given me in the preparation of this paper, and in particular for his skill and patience in preparing the illustrations. For the loan and gifts of specimens used in this work, I gratefully acknowledge the cooperation of the Curator of Fishes, Museum for Naturkunde, Humboldt-Universität, Berlin (D.D.R.); Dr R. A. Jubb and Mr P. S. Skelton, Albany Museum, South Africa; Dr D. F. E. Thys van den Audenaerde, Musee Royal de l'Afrique Centrale, Tervuren; Dr J.-P. Gosse, Institut Royal des Sciences Naturelles de Belgique, Brussels; Dr M. L. Bauchot, Museum National d'Histoire Naturelle, Paris; Dr H. Wilkens, Zoologisches Institüt und Zoologische Museum, University of Hamburg; Dr J. E. Böhlke, Academy of Natural Sciences, Philadelphia; and Dr M. J. Penrith, State Museum, Windhoek.

Finally, it is my pleasure to thank my colleagues of the freshwater fish section (then including Dr Richard Vari, a NATO postdoctoral research fellow) for the innumerable arguments we have had on the subject of phylogenetic systematics.

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Manuscript accepted for publication 20 April 1978

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Bulletin of the
British Museum (Natural History)

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Zoology series Vol 35 No 5 28 June 1979

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

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This number completes volume 35

ISSN 0007-1498

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Zoology series
Vol 35 No 5 pp 323-363

Issued 28 June 1979

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Synopsis

A detailed account is presented of the external morphology of the British representatives of the genus *Phthiracarus*. The literature relating to the genus is reviewed and the status of certain of the older species considered. Thirteen British species, seven of which are considered to be new, are described, figured and keyed. Of these, only *P. affinis* (Hull), *P. anonymum* Grandjean and *P. murphyi* Harding were known previously from the British Isles, while *P. laevigatus* (C. L. Koch), *P. nitens* (Nicolet) and *P. tardus* Forsslund are recorded for the first time. A neotype for *P. affinis* is designated. On the basis of the chaetotactic pattern of the legs it is suggested that the genus could be divided into two species groups.

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Issued 28 June 1979

Introduction

The genus *Phthiracarus* comprises free-living ptychoid mites occurring predominantly in the upper layers of highly organic forest soils. Containing about 70 nominate species (see Appendix 1), it is the largest of the Euptyctimoid genera and in many respects the most difficult to study. Apart from *P. anonymum* Grandjean and certain of the more recently described species (notably *P. murphyi* Harding), the original descriptions have been somewhat superficial and it is even doubtful whether some of the nominate species listed in Appendix 1 have been correctly assigned to *Phthiracarus*. Partial revisions of the genus have been published by Jacot (1930, 1936, 1938 & 1939), Feider & Suciu (1957) and van der Hammen (1963 & 1964) but only two of the species redescribed, namely, *P. laevigatus* (C. L. Koch) and *P. nitens* (Nicolet), can now be positively identified. The only substantial keys to the genus are those published by Willmann (1931), Sellnick (1960), and Gilyarov & Krivolutsky (1975), all of which employ characters that have proved generally to be useless for species differentiation.

Materials and methods

This revision is based on a comprehensive survey of the literature and detailed morphological studies of all the available *Phthiracarus* material from widely separated areas in the British Isles. A large part of the material was taken from the unnamed and unsorted collections of the British Museum (Natural History). Additional material was obtained from a series of fermentation and humus layer samples collected under stands of beech, larch, oak, Scots pine and Sitka spruce at the following four areas: The Woburn Estate, Bedfordshire; New Forest, Hampshire; Tintern Forest, Monmouthshire; Alice Holt Forest, Surrey. These four areas were sampled during the period April 1972 to October 1973 as part of a study designed to compare the effects of hardwood and coniferous tree species on populations of Euptyctima and full descriptions of the sampling sites will be published elsewhere. The mites were extracted using a 'controlled-gradient' funnel apparatus similar to that described by Macfadyen (1961). All the available type material of *Phthiracarus* species has also been examined.

For detailed studies of the external morphology, the mites were cleared and softened by heating in a test tube of 75% lactic acid in a boiling water bath, the duration of heating being dependent on the degree of sclerotization. Each mite was then transferred to a small quantity of Berlese's fluid on a slide and dissected using two fine needles. Cavity slides containing lactic acid were used for temporary preparations of the aspis, notogaster, ventral plates and ovipositor. Permanent preparations of the legs, chelicerae and infracapitulum requiring examination under oil immersion were made on plain slides in Berlese's fluid.

For each species measurements were taken from all the available specimens. The length of the aspis was taken along the mid-dorsal line and the greatest width as the transverse distance between the antiaxial margins of the bothridia. The sensillus, interlamellar and lamellar setae were measured with the aspis mounted dorsally and the rostrals with the aspis positioned laterally. The notogaster was measured in lateral aspect and the length was taken from the anterodorsal limit of the collar to a point just ventral to seta h_1. The greatest depth of the notogaster was measured between the seta e_1 and the ventral margin. Each chelicera was measured from the base of the principal segment to the end of the fixed digit. For detailed study of the leg chaetotaxy, the legs were positioned laterally.

Morphological studies were also undertaken using the scanning electron microscope – good results being obtained using air-dried spirit-preserved material. Any foreign matter adhering to the specimens was first removed by brief treatment in an ultrasonic bath. The mites were then soaked in a small quantity of an anti-static solution of 0·5% 'Duron' in isobutyl alcohol for a period of 12–24 h (Sikorski *et al.*, 1967). It was found that this treatment eliminated any 'charging' due to incomplete coating of cavities such as the bothridia. After soaking, the specimens were removed from the solution, washed in isobutyl alcohol and allowed to dry. The mites were stuck onto specimen stubs using double-sided adhesive tape and coated with a 20 nm layer of evaporated gold.

External morphology

The following account of the external morphology of *Phthiracarus* refers to the adult only; full descriptions of the immature stages will form the basis of another paper. The setal nomenclature used in the later works of Grandjean has been followed throughout the account.

Idiosoma

Aspis; Fig. 1B–D; Pl. 1a, e): A pair of oval weakly-sclerotized areas anterodorsally marks the positions of the retracted chelicerae. The ventral margin of the aspis is reflexed to form the *aspal rim* (*a.r.*) and there is a distinct *lateral ridge* (*l.r.*). The *bothridium* (*b.*) has an inner multi-chambered wall and a smooth outer one from which three finger-like chitinous *tracheoles* arise and are directed mid-dorsally. The margin of the bothridial aperture is thickened (as shown by the arrow in Pl. 1e) and flanked posteriorly by a pronounced scale. There are three pairs of procumbent dorsal setae, the *rostrals* (*ro*), *lamellars* (*la*) and *interlamellars* (*il*), and two pairs of setae laterally, the *exobothridials* (*ex*) and the *sensilli.* In most of the species examined, setae *il* and *la* are located at the level of the bothridia, *la* being somewhat shorter than *il.* The sensilli are variable in form and so provide a useful taxonomic feature. In some species they are short, ovate or lanceolate while in others they are long, narrow and tapering. The sensillar margin may be serrated (Pl. 1a) and in *P. serrulatus* sp. nov. it bears a number of straight-edged teeth subterminally. The sensillus is most easily observed in scanning electron micrographs as in flattened slide preparations its appearance can depend very much on orientation.

Notogaster (Fig. 1A, E; Pl. 1e): The anterior margin of the notogaster is well sclerotized and, following Jacot (1930), can be subdivided into three regions: the thickened *collar* (*C*), the *pseudostigmatic* [*sensillar*] *notch* (*N*) (Pl. 1e) and the *lappet* (*L*) which projects somewhat anteriorly. Of the 15 pairs of setae, 14 are regarded as being homologues of c_{1-3} and cp, d_{1-2}, e_{1-2}, h_{1-3} and ps_{1-3} of the holotrich nomenclature, and the additional seta as ps_4. The distributional pattern of notogastral setae is essentially similar in all the British species but the relative lengths and attitudes of the setae vary considerably from one species to another. The vestiges of setae (f_1) and (f_2) are thought to be represented by two pairs of subcuticular structures located posterolaterally (Grandjean, 1950). Vestigial f_1 normally lies between setae h_1 and ps_1 and f_2 between setae h_1 and h_2 but in certain small species (for example, *P. serrulatus*) f_1 is closely associated with the seta h_1. There are four pairs of prominent subcuticular fissures: the *anteriors* (*ia*) and *medians* (*im*) are situated just posterior to seta *cp* while the *posterior pleurals* (*ip*) and *infrapleurals* (*ips*) (when present) are situated on either side between setae h_2 and h_3 and between setae ps_3 and ps_4 respectively.

Ano-genital region (Figs 2E; 3B; Pl. 1b): On each *anal plate* there are five setae. Two *anal setae* an_{1-2} are located on the paraxial margin and three *adanals* ad_{1-3} submarginally; setae ad_{1-2} are often vestigial. Each anal plate has a prominent hood-like lobe located ventro-anteriorly on its paraxial margin and in the so-called 'left fitting' arrangement (van der Hammen, 1963) the lobe on the right-hand plate overlaps that on the left-hand plate while in the 'right fitting' arrangement (as shown by the arrow in Fig. 2E) the reverse is true. Van der Hammen has suggested that the arrangement of these interlocking lobes and the condition of setae ad_{1-2} (present or vestigial) could be useful taxonomic features. This view is not, however, supported by the present study since these two features have been found to exhibit considerable intraspecific variation.

On each *genital plate* there are two well-developed anterior ridges separated by a median furrow. The furrow bears a single *aggenital seta* ag_1 antiaxially (Pl. 1b). There are nine *genital setae* arranged in two rows. The anterior five setae g_{1-5} are minute and located on the paraxial border while the posterior four setae g_{6-9} are moderately short and submarginal. There are three pairs of *genital papillae* (*g.p.*), the anterior pair being rather small. Elongate oval structures have been observed inside the genital papillae and these may prove to be spermatophores. The first two pairs of genital papillae border the *ovipositor*, which, when fully extended, can be seen to be a rather short tube divided into a distal and a proximal portion by a weak circular constriction.

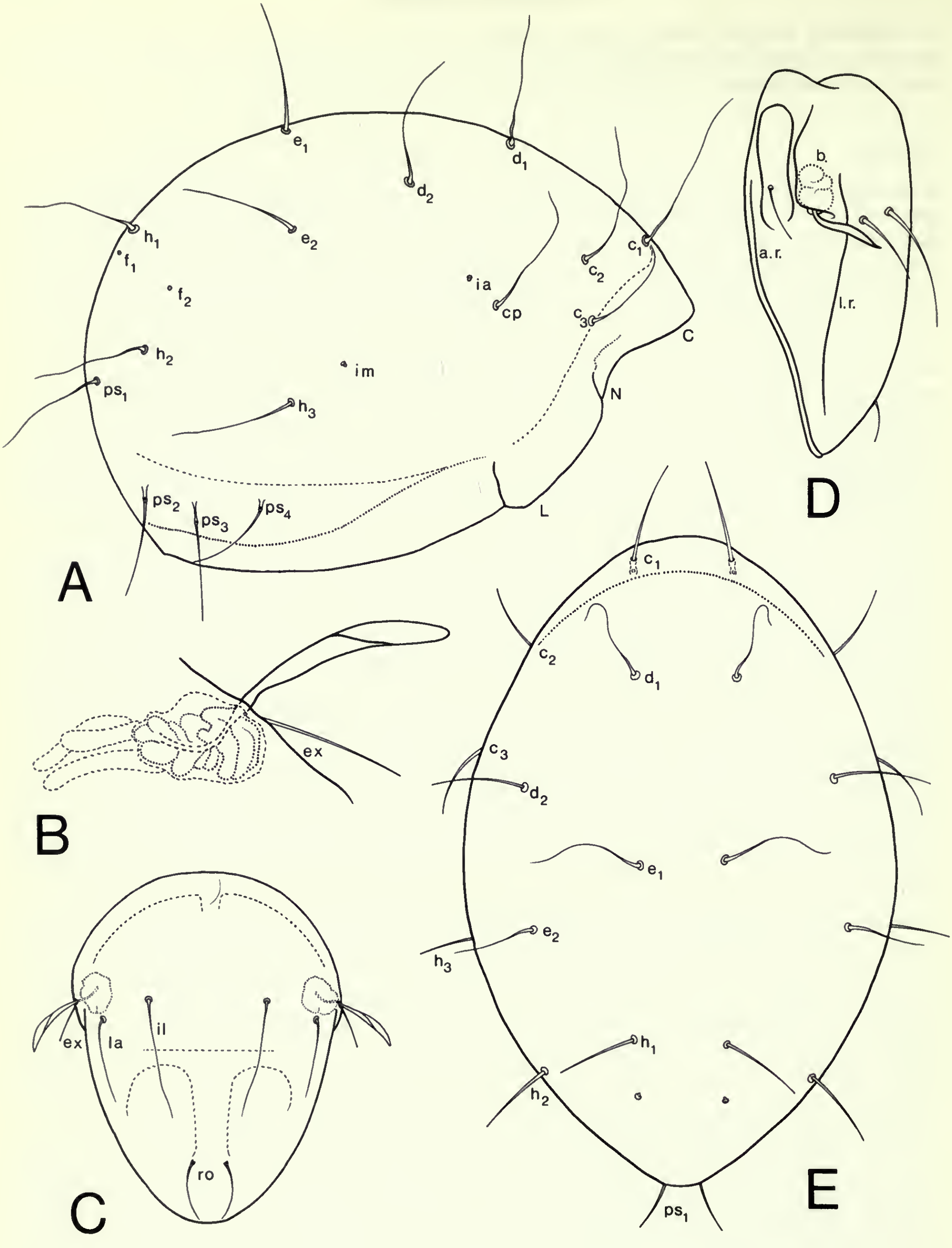
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Fig. 1 *Phthiracarus affinis*: (A) notogaster, lateral; (B) sensillus and bothridium; (C) aspis, dorsal; (D) aspis, lateral; (E) notogaster, dorsal.

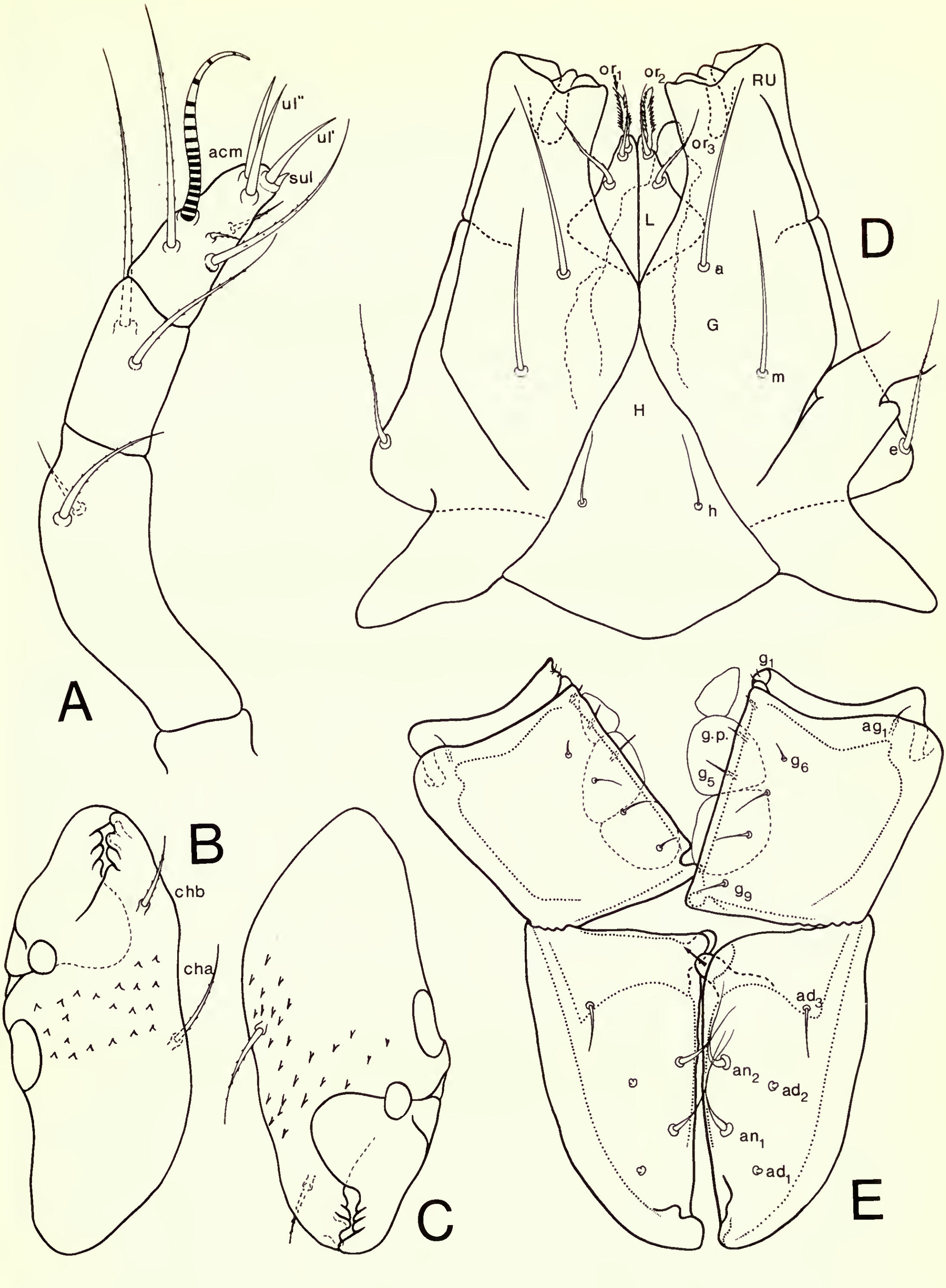
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Fig. 2 *Phthiracarus affinis*: (A) pedipalp; (B) chelicera, antiaxial; (C) chelicera, paraxial; (D) infracapitulum, ventral; (E) ano-genital region.

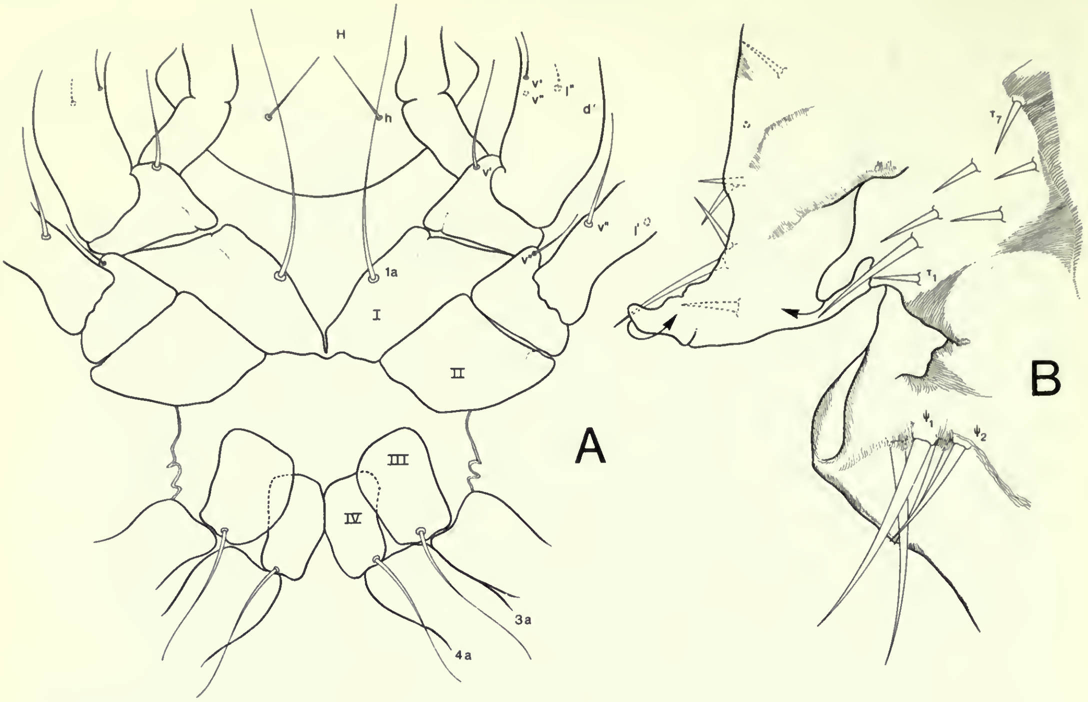

Fig. 3 *Phthiracarus affinis*: (A) coxisternal region; (B) ovipositor, lateral.

The six *coronal* (*k*) setae which Grandjean (1956) found on the constriction in *Heminothrus targionii* (Berlese) and in the 'higher' oribatid mite *Eremaeus hepaticus* C. L. Koch are apparently absent in all the British *Phthiracarus* species. The surfaces of both portions of the ovipositor are strongly pleated. Distally, three eugenital lobes surround the opening of the ovipositor: an unpaired ventral lobe and a pair of laterodorsal lobes (as shown by the arrows in Fig. 3B). The ventral lobe is triangular in anterior view and bears two pairs of setae distally (ψ_{1-2}), the posterior pair (ψ_2) being the shorter. The two laterodorsal lobes are larger, compressed laterally, and each bears seven setae (τ_{1-7}) antiaxially.

Feider & Suciu (1957) figured two pairs of setae, presumably (ψ_1) and (ψ_2), on the ovipositor of *P. lentulus* (C. L. Koch), and in *P. parabotrichus* Feider & Suciu, a dorsal group of seven setae and a smaller ventral group of three setae were shown, possibly (τ) and (ψ) respectively. Harding (1976), in his description of *P. murphyi*, identified 16 setae on the ovipositor: three setae on each of the laterodorsal lobes, two setae on the ventral lobe and six setae which he considered as the coronals.

Gnathosoma

INFRACAPITULUM (Fig. 2D; Pl. 1c): The *lateral lips* (*L*) bear three pairs of *adoral setae* (or_{1-3}), the anterior pair (or_1) being brush-like (Pl. 1c) and the two posterior pairs weakly serrated. The infracapitulum is 'sternarthrous' (Grandjean, 1957) and the *rutella* (*RU*) are without atelobasic expansions. There are three pairs of *infracapitular setae*: an *anterior* (*a*) and a *median* pair (*m*) of long smooth setae located on the *genae* (*G*) and a rather short posterior pair (*h*) located on the *hysterostoma* (*H*). Laterally there is a single pair of barbed *supracoxal setae* (*e*).

PEDIPALPS (Fig. 2A; Pl. 1d): The pedipalps are only three-segmented. The basal segment, formed from the fused trochanter, femur and genu, bears two setae, the tibia two setae and the tarsus seven setae and a solenidion. The three most distal of the tarsal setae are eupathidial: the *anteroculminal acm*, *anterior ultimal ul′* and *posterior ultimal ul″*. The *subultimal seta sul* is a minute spine-like process at the base of seta *ul′* (as shown by the arrow in Pl. 1d) and also appears to be eupathidial.

CHELICERAE (Fig. 2B, C): Both the fixed and the movable digits are dentate. The movable digit has four teeth and the fixed digit carries five. The latter are arranged in two rows, an outer one of two and an inner one of three teeth. The large principal segment which terminates in the fixed digit, bears a number of short conical spines on the antiaxial surface and a larger number of sharply pointed spines paraxially; the spines are distributed extensively on the paraxial surface but are restricted to a more compact zone antiaxially. There are two *cheliceral setae*, an *anterior seta chb* inserted on the antiaxial surface and a *posterior seta cha* located dorsally. Both setae are serrated, *cha* being somewhat longer than *chb*.

Legs

Legs II to IV are approximately equal in length while leg I is longer and more robust. The individual epimera are separate and, except for epimera II, each bears a single seta, 1*a*, 3*a* and 4*a* respectively (Fig. 3A). All the legs have five segments: the trochanter, femur, genu, tibia and tarsus, and terminate in a single claw bearing two ventral teeth and an antero- and posterolateral row of serrations (Pl. 2c).

SOLENIDIA (Pl. 2a, b, e): The solenidiotaxy (I 2–1–3; II 1–1–2; III 1–1–0 and IV 0–1–0) is constant in the 13 species examined and typical of that found in other Phthiracaridae. All the

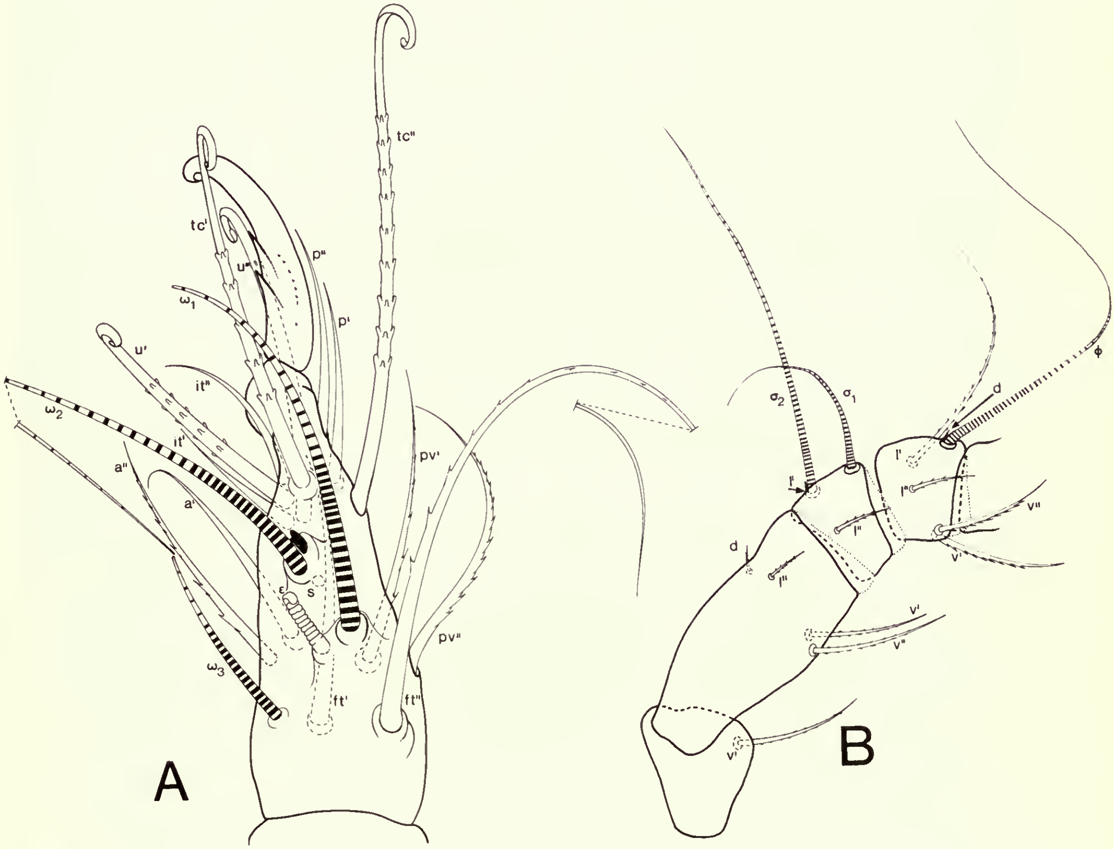

Fig. 4 *Phthiracarus affinis*, leg I: (A) tarsus, dorsal aspect; (B) trochanter to tibia, posterolateral aspect.

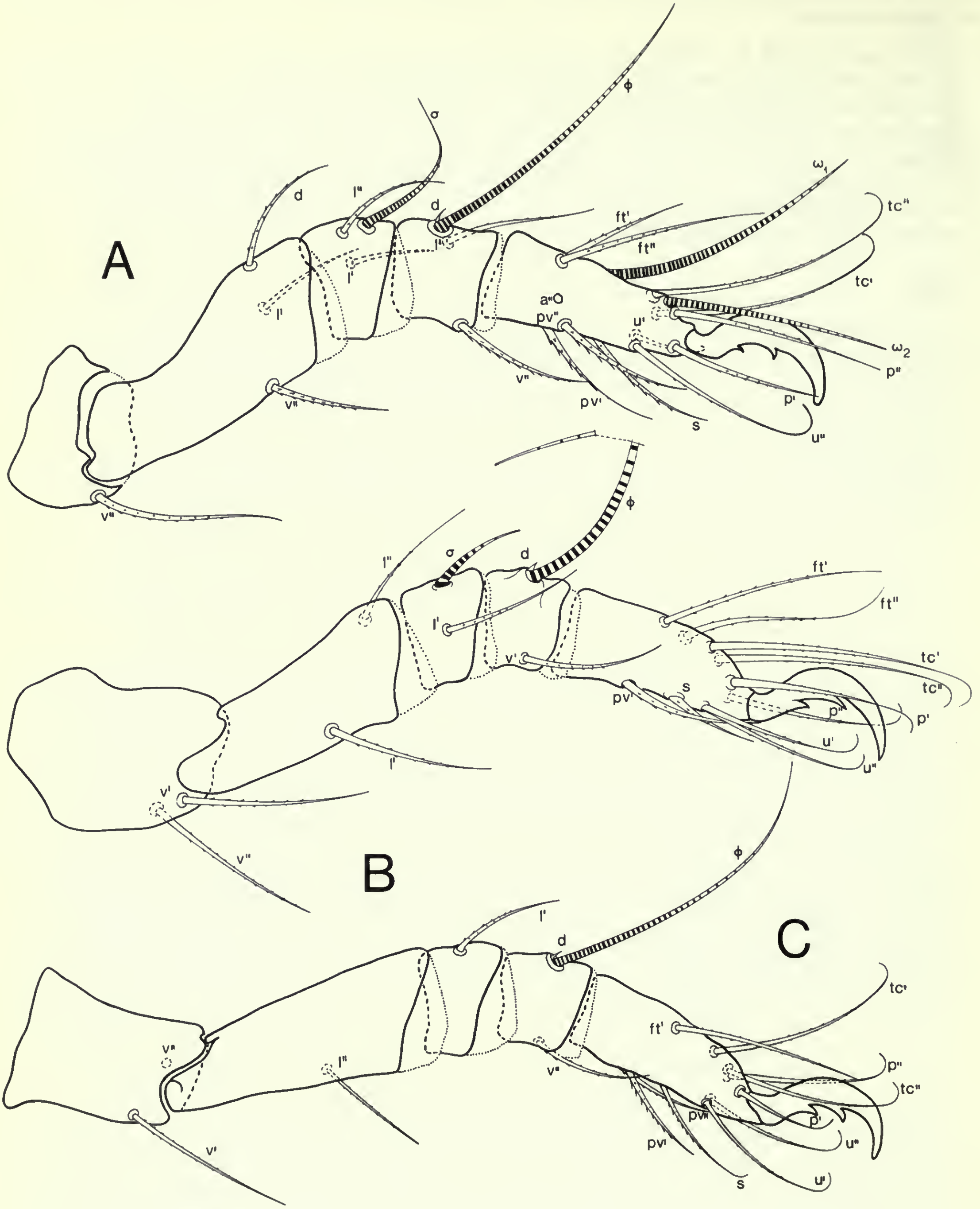
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Fig. 5 *Phthiracarus affinis*, legs II–IV; (A) leg II, posterolateral aspect; (B) leg III, anterolateral aspect; (C) leg IV, anterolateral aspect. (Fig. 5A–C are drawn at the same magnification.)

tarsal solenidia are transversely striated as described by Grandjean (1935) for *Oribotritia berlesei* (Michael). On tarsus I the solenidion ω_1 is closely associated with the famulus ε (Pl. 2a) which is short and rugose. Solenidion ω_2 is the longest of the three tarsal solenidia and has a small distal coupling seta (Pl. 2b). Harding (1976) described such a setal/solenidial association in *P. murphyi* and in *P. nitens* but noted that solenidion ω_2 was apparently free in *P. anonymum*. In the present study the scanning electron microscope has revealed the presence of a distal coupling seta in all the British species. Although usually short and simple, in *P. rectisetosus* sp. nov. this seta is long, prominent and apparently divided into two parts by a longitudinal constriction, the distal part being produced into a scabre-shaped process reminiscent of that found in species of the genus *Steganacarus* (see Parry, 1978). On all legs the tibial solenidion φ is coupled with a reduced dorsal seta (Pl. 2e) while on genu I solenidion σ_2 is coupled with a reduced lateral seta.

LEG SETAE (Figs 4; 5; 14; Pl. 2d): In all the larger species examined the formulae for the leg setae are: I (1–4–2–5–16–1); II (1–3–2–3–12–1); III (2–2–1–2–10–1) and IV (2–1–1–2–10–1). This complement will be referred to as the 'complete chaetotaxy type' (Figs 4; 5). On tarsus I only 16 of the 20 setae regarded by Grandjean (1940) as being characteristic of 'higher' Oribatei are present, the *primilaterals* and *postlarvals* always being absent. Four setae surround the base of the claw, namely, a dorsal pair of *prorals* (*p*) and a ventral pair of *unguinials* (*u*). Three pairs of setae are located posterodorsally to the prorals: the *iterals* (*it*), *tectals* (*tc*) and *fastigials* (*ft*). Ventrally, behind the unguinials, there is an unpaired *subunguinial* seta *s* and a pair of *primiventral* setae (*pv*). A single pair of *anterolateral* setae (*a*) is located laterally behind the prorals and the unguinials.

On tarsi II to IV there is a reduction in the number of setae to 12, 10 and 10 respectively: setae (*it*), *a*′ and ε are absent on tarsi II to IV, seta *pv*″ on tarsus III, seta *a*″ on tarsi III and IV and seta *ft*″ on tarsus IV. Furthermore, the tarsal setae exhibit considerable variety in form. On tarsus I six of the setae (*s*, (*it*), (*p*) and *a*′) are hollow eupathidia. On all four tarsi setae (*ft*) and (*pv*), together with *a*″ on tarsi I and II, are generally more or less straight, circular in section and bear two or three rows of lateral serrations. In certain species (for example, *P. globus* sp. nov.) seta *ft*″ on tarsus II is hooked distally. The other tarsal setae, (*tc*) and (*u*) on tarsus I and (*tc*), (*u*), (*p*) and *s* on tarsi II to IV, are ribbon-like, hooked distally and covered with whorls of spicules in the middle third. Such setal ornamentation is, however, only discernible in the larger species of the genus.

The setation of the four proximal leg segments is shown in Table 1. Apart from tibia I which bears a whorl of five setae (*d*, *l*′, *l*″, *v*′ and *v*″), each of the other segments bears an incomplete whorl of one to four setae. Seta *d* on femur I is somewhat thickened, serrated and curved distally (Pl. 2d) in all the species examined except *P. clavatus* sp. nov. and *P. globus* sp. nov. where it is rather long, straight and only weakly serrated. On all segments setae (*l*) and (*v*) carry two or three rows of serrations.

Table 1 Chaetotaxy of the four proximal leg segments in *Phthiracarus*

Segment	Leg I	II	III	IV
Tibia	d, l′, l″, v′, v″	d, l′, v″	d, v′	d, v″
Genu	l′, l″	l′, l″	l′	l′
Femur	d, l″, v′, v″	d, l′, v″	l′, l″	l″
Trochanter	v′	v″	v′, v″	v′, v″

In all the smaller species of the genus (for example, *P. tardus* Forsslund) there are fewer setae on legs I, II and IV (Fig. 14): tarsus I bears 15 setae (*a*′ absent), tarsi II and IV usually bear 11 and 9 setae respectively (*s* absent), femur I bears 3 setae (*v*′ absent) and genu IV is without any setae (*l*′ absent). Thus the setal formulae (referred to here as the 'reduced chaetotaxy type') are: I (1–3–2–5–15–1); II (1–3–2–3–11–1); III (2–2–1–2–10–1) and IV (2–1–0–2–9–1). In *P. anonymum* (a variant of the 'reduced chaetotaxy type') the number of setae on tarsus IV is further reduced by the absence of seta *pv'*. Although the total number of setae on leg III is constant throughout the genus, in species of the 'complete chaetotaxy group' seta *pv"* is absent and seta *s* present while the reverse is true in the 'reduced' group.

Review

Perty proposed the genus *Phthiracarus* in 1839 and two years later created the 'family' Phthiracarea (now Phthiracaridae) for the single species *P. contractilis*. Perty's original specimens are presumed to be lost and his figures (subsequently published by Claparède, 1868) and description are such as to make the specific identity of *contractilis* impossible to determine.

Acarus piger Scopoli, 1763, the oldest species currently classified in *Phthiracarus*, was originally assigned to the genus by Oudemans (1915). The mite described by Scopoli, for which there is no type material available, is undoubtedly ptychoid but there is no evidence to suggest that it is a species of *Phthiracarus* – it is probably a member of the Euphthiracaroidea (see Jacot, 1930).

The systematic position of *Oribates dasypus* Dugès, 1834 is also somewhat uncertain although the species is evidently ptychoid. Michael (1888) recorded *dasypus* in the British Isles. The specimen labelled *Hoplophora** *dasypus* from Theydon Bois in the Michael Collection (deposited in the BMNH) is *P. clavatus*.

In 1841 ten species of *Hoplophora*, nine† of which are currently classified in *Phthiracarus*, were described by Koch from woodland habitats near Regensburg. While it seems probable that these mites have been correctly assigned to *Phthiracarus* (with the ecxeption of *H. testudinea* which is possibly a member of the Euphthiracaroidea), only two of Koch's descriptions refer to 'key characters' which might permit certain reidentification. In comparison with the other Regensburg species, *H. globosa* is very 'globular' while in *H. laevigata* the notogaster is 'angled' at the level of seta c_1. The remaining six species can only be divided into two groups on the basis of their notogastral setae; *crinita*, *ferruginea* and *longula* are each characterized by 'long setae' while the other three species (*lentula*, *lucida* and *straminea*) are all described as being 'sparsely setose'. Despite the inadequacy of Koch's descriptions and the apparent absence of any type material, various interpretations of his species have been published, amongst others by Jacot and van der Hammen. In *Les Phthiracaridae de Karl Ludwig Koch*, Jacot (1936) redescribed six species from topotypic material but neglected details of the leg and notogastral chaetotaxy, now regarded as being essential for the separation of *Phthiracarus* species. More recently, van der Hammen (1963), in one of his series of papers on the Phthiracaridae, has published a detailed description of *P. laevigatus* (from material collected at Regensburg) and has designated a neotype. Van der Hammen (personal communication) also believes that he has topotypic material of Koch's seven other species but until these specimens have been examined it seems advisable to postpone any decision concerning their taxonomic status.

Hoplophora nitens Nicolet (1855), recorded as common in the woods around Paris, is a *Phthiracarus* species. The true identity of *nitens* appears to be doubtful, although van der Hammen's redescription (see Hammen, 1964) from topotypic material is generally accepted.

Hoploderma italicum Oudemans (1907), recorded from Tiarno, Italy, is not based on a type specimen but on Berlese's description of *H. dasypus* which Oudemans regarded as being distinct from *O. dasypus* Dugès. Van der Hammen (1952) considers the specimens of both Berlese and Oudemans as being useless for reidentification purposes.

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* Certain species now assigned to *Phthiracarus* have in the past been classified in two other genera, *Hoplophora* C. L. Koch and *Hoploderma* Michael. The genus *Hoplophora* was erected by Koch in 1836 for two species, *H. decumana* C. L. Koch and *H. stricula* C. L. Koch, currently classified in *Oribotritia* and *Steganacarus* respectively. In 1841 Koch described further species of *Hoplophora* but did not publish a diagnosis of the genus or designate a type (*H. laevigata*) until the following year. Jacot's 1928 application to the International Commission on Zoological Nomenclature for a ruling on the validity of the type designation (Koch, 1842) for a genus first published six years earlier (Koch, 1836) was not published until 1946 (see Jacot, 1946). The Commission's subsequent ruling (I.C.Z.N., 1953) allowed *H. laevigata* to be retained as the type (*H. laevigata* is here regarded as a species of *Phthiracarus*) since the genus was not originally monotypic and did not contain a species called *typus* or *typicus*. However, the generic name *Hoplophora* had been found by Michael (1898) to be preoccupied by *Hoplophora* Perty, 1833 (Neuroptera), and the new name *Hoploderma* was proposed.

† The tenth species of *Hoplophora*, *H. ardua*, is now classified in *Rhysotritia*.

Hoploderma boreale Trägårdh (1910) and *Hoploderma affine* Hull (1914) are both *Phthiracarus* species. This is evident from the figures of these mites and has been confirmed by examination of 'cotype' and syntype material respectively. The characteristic features of these two species are now certain.

Oudemans (1915) proposed the name *Phthiracarus undatus* for the 'larve' of *Hoplophora stricula* (*sensu* Nicolet, 1855). While Nicolet's figures and description appear to refer to an adult oribatid mite, there is no evidence to suggest a *Phthiracarus* species.

Berlese (1920 & 1923) described six species of *Phthiracarus*: *rotundus*, *roubali* and *subglobosus* are European while *P. nigerrimus* was collected from Argentina, *P. curtulus* from the United States and *P. pudicus* from South Africa. The type of each of these species has been examined by Dr J. G. Sheals (BMNH) who has found that their condition is such as to make any chaetotactic characters impossible to discern. In 1959 van der Hammen reviewed all Berlese's species of primitive oribatid mites deposited in the 'Stazione di Entomologia Agraria', Florence, but could not confirm the identities of any of the *Phthiracarus* species.

Jacot (1928–1939) described 13 species from North America and a single species (*P. insularis*) from the Marquesas Islands. Of these, type material is available for eight species (see Appendix 1), seven of which are represented by a number of 'cotypes' while only *P. brevisetae* is based on a holotype. All Jacot's *Phthiracarus* specimens are mounted in Canada Balsam, the majority being entire and uncleared. The shape of the sensillus and the relative lengths and attitudes of the dorsal notogastral setae can usually be seen in such preparations but the leg chaetotaxy is extremely difficult to study. In view of the condition of Jacot's material, it seems advisable to postpone any decision regarding the identities of his *Phthiracarus* species until all the type specimens have been dismounted and cleared (an exercise which will be complicated by the presence on each 'cotype' slide of additional species of this and other genera). It can, however, be noted that *P. brevisetae* appears to be close to if not conspecific with *P. laevigatus*, while the differences between *anonymus amicus* and Grandjean's *anonymum* are evidently not sufficient to warrant subspecific ranking. *P. insularis* and *P. setosellum bryobium* possibly have affinities with two British species, *P. murphyi* and *P. clavatus* respectively.

In 1933 Grandjean published the first of a series of detailed works on the external morphology of *P. anonymum*, a species he recorded from rotting wood in his cellar at Périgueux, Dordogne, France. By clearing whole and dissected specimens (Grandjean, 1949) he was able to observe the patterns of setae on the body shields (Grandjean, 1933, 1934 & 1950), which provided new criteria for the identification of species of this genus. Hitherto, species differentation had been based almost entirely on body shape and colour, two characters now known to be uniform in many *Phthiracarus* species. Grandjean (1935, 1940 & 1946) also undertook the first detailed studies of the leg chaetotaxy of oribatid mites, introducing the system of nomenclature now in general use. However, in recent years the majority of *Phthiracarus* species have been defined solely in terms of characters visible in undissected material. Leg chaetotactic characters have only rarely been studied (van der Hammen, 1963; Sheals, 1965; Ramsay, 1966; Harding, 1976) probably due to difficulties in interpretation.

Further *Phthiracarus* species have been described by Willmann (1932, 1939 & 1951), Woolley (1954) and Forsslund (1956) (see under Descriptions of species). However, *P. peristomaticus*, recorded by Willmann (1951), from a number of habitats including leaves, turf and subsoil under buckthorn, guelder-rose and alder, nördlich Moosmühle, near Vienna, Austria, cannot be identified either from Willmann's figure or from his description. Moreover, there are no specimens of *P. peristomaticus* in Willmann's Collection (Dr W. Hirschmann, personal communication). Feider *et al.* (1957, 1958 & 1968) recorded eight species from Rumania, none of which were described in sufficient detail to permit certain reidentification, although *P. baloghi*, collected from oak leaves in Iaşi, appears to be unique among described species of the genus in having notogastral setae of two markedly different lengths. Unfortunately, it has not been possible to borrow the types of any of the Rumanian species for study. This was also the case with species described by Balogh (1958, 1962, 1963 & 1977) and Krivolutsky (1966 & 1975). Other *Phthiracarus* species have been described from Japan (Aoki, 1958 & 1963), Chile (Hammer, 1962), Nepal (Sheals, 1965), New Zealand (Ramsay, 1966), Spain (Pérez-Iñigo, 1969), Tahiti (Hammer, 1972), the

Tonga Islands (Hammer, 1973) and the British Isles (Harding, 1976) (see Appendix 1). Of these, *P. robertsi*, recorded by Sheals from rhododendron litter in Nepal, is of particular interest for, although having certain affinities with *Phthiracarus*, it shows a general similarity to *Steganacarus*. The arrangement of setae on the genital and anal plates, while reminiscent of *Phthiracarus*, is nevertheless 'unusual' for setae ad_{1-3} are almost marginal. The only diagnostic feature which *P. robertsi* appears to share with all species of the genus is the presence of a coupled solenidion on tibia IV. The general shape of the aspis and the form of the integumental ornamentation are characteristic of *Steganacarus* species and it is questionable whether *P. robertsi* should have been classified in *Phthiracarus* (see Sheals, 1969).

There have been relatively few reviews of the British species. In his *Synonymic catalogue of British Acari*, Turk (1953) listed only five species of *Phthiracarus*: *piger* (Scopoli) (=*Hoplophora dasypus* Dugès *sensu* Michael), *affine* (Hull), *anonymum* Grandjean, *ligneus* Willmann and *spinosum* (Sellnick) (now classified in *Steganacarus*). Turk does not give sources for individual records but the above are presumably based on the following published records: Michael, 1888, Halbert, 1915 and Hull, 1916 (*dasypus*); Hull, 1914 (*affine*); Murphy, 1954 (*anonymum*); Macfadyen, 1952 (*ligneus* and *spinosum*). Of these, only *P. affinis* and *anonymum* are recognized in the present revision since the taxonomic status of the other two *Phthiracarus* species is doubtful.

Descriptions of species

Genus *PHTHIRACARUS* Perty

Hoplophora Koch, 1836 : Hft. 2, Nr. 9. Preoccupied name (Michael, 1898 : 77). Type, by subsequent designation, *Hoplophora laevigata* Koch, 1841 : Hft. 38, Nr. 16.

Phthiracarus Perty, 1839 : column 847. Type, by monotypy, *Phthiracarus contractilis* Perty, 1841 : 874. Figured by Claparède, 1868 : pl. 36, figs 15–19.

Hoploderma Michael, 1898 : 77. Proposed as replacement name for *Hoplophora* Koch.

DEFINITION: Weak to heavily sclerotized Phthiracaridae ranging in length from about 350 – 1300 µm (lateral measurement taken in closed position). The integument of the dorsal and ventral shields, infracapitulum and chelicerae is densely punctate while that of the appendages is smooth. The interlamellar and lamellar setae are procumbent and the aspis without a median keel. The notogaster bears 15 pairs of fine and generally smooth setae. Fissures *ip* and *ips* may be present or absent. The notogaster bears neither a cowl nor a carina. Two pairs of anal setae are located on the paraxial margins of the anal plates and three pairs of adanals submarginally (the exception being *P. anonymum* with three pairs of setae located marginally). All are usually more or less equal in length although the two posterior pairs of adanal setae may be vestigial. The genital setae are arranged in a pattern of 5+4 along the paraxial margins of the genital plates. On leg IV the tibial solenidion is coupled.

DIAGNOSIS: *Phthiracarus* is distinguished from other genera of the Phthiracaridae by having a combination of procumbent interlamellar setae and a 2+3 arrangement of setae on the anal plates.

Key to adults of the British species of the genus *Phthiracarus*

Only two species can be recognized on the basis of a single character. In *P. anonymum* seta ad_3 is located marginally (submarginally in all other species) while *P. laevigatus* appears to differ from all the other members of this genus in that the notogaster is strongly arched at the level of seta c_1.

It has been concluded from an investigation of the external morphology of the British species that the number of setae on femur I (4 or 3) and genu IV (1 or 0), the shape of the sensillus, the presence or absence of fissures *ip* and *ips* and the relative lengths and attitudes of the notogastral setae are the most useful characters for species differentiation. These are the main characters used in the following key.

1 Femur I with four setae (Fig. 4B); genu IV with a single seta (Fig. 5C) 2
– Femur I with three setae (Fig. 14B); genu IV without setae 9
2 Notogastral fissures *ip* and *ips* absent (Fig. 1A) 3
– Notogastral fissures *ip* and *ips* present (Fig. 10D) 6

3 Sensillus about 80 µm long, narrow and pointed distally (Pl. 4d); notogastral setae shorter than $c_1 - d_1$ . . . . ***P. juvenalis*** sp. nov. (p. 342)
– Sensillus not of this form; notogastral setae equal to or greater than $c_1 - d_1$ 4
4 Notogastral setae procurved (Fig. 7A); sensillus as in Pl. 3f . . ***P. clavatus*** sp. nov. (p. 338)
– Notogastral setae erect 5
5 Large species, notogaster over 550 µm in length; seta *d* on femur I straight ***P. globus*** sp. nov. (p. 341)
– Smaller species, notogaster under 500 µm in length; seta *d* on femur I curved distally (Pl. 2d) ***P. affinis*** (Hull) (p. 335)
6 Notogaster sharply angled at the level of seta c_1 when viewed laterally (Fig. 10D) ***P. laevigatus*** (C. L. Koch) (p. 344)
– Notogaster rounded anteriorly when viewed laterally (Fig. 1A). 7
7 Sensillus 50–60 µm long, narrow and finely serrated (Fig. 12A); notogastral setae shorter than $c_1 – d_1$ and procurved. . . . . ***P. nitens*** (Nicolet) (p. 346)
– Sensillus not of this form; notogastral setae equal to or greater than $c_1 – d_1$. 8
8 Notogastral setae procurved; on tarsus I seta coupled with solenidion ω_2 much shorter than famulus . . . . ***P. murphyi*** Harding (p. 346)
– Notogastral setae almost erect; on tarsus I seta coupled with solenidion ω_2 almost as long as famulus . . . . ***P. rectisetosus*** sp. nov. (p. 348)
9 Notogaster with vestigial f_1 just dorsal to seta h_1 (Fig. 6E); seta ad_3 located on paraxial margin of anal plate (Pl. 3e); tarsus IV with eight setae (Fig. 6B) ***P. anonymum*** Grandjean (p. 336)
– Notogaster with vestigial f_1 located on a level with or ventral to seta h_1; seta ad_3 located submarginally on anal plate (Fig. 2E); tarsus IV with nine setae (Fig. 14D). . . . 10
10 Sensillus about 70 µm long 11
– Sensillus 30–40 µm long 12
11 Sensillus with membranous border (Fig. 11B). . . . . ***P. membranifer*** sp. nov. (p. 344)
– Sensillus serrated distally (Fig. 13B) . . . . . . ***P. serrulatus*** sp. nov. (p. 348)
12 Notogastral setae equal to $c_1 – d_1$ and erect; tarsus II with 12 setae . ***P. tardus*** Forsslund (p. 351)
– Notogastral setae greater than $c_1 – d_1$ and slightly flexuose (Fig. 7F); tarsus II with 11 setae ***P. flexisetosus*** sp. nov. (p. 340)

Phthiracarus affinis (Hull)

(Figs 1; 2; 4; 5; Pls 2a, b, d; 3a, d)

Hoploderma affine Hull, 1914 : 287, pl. C9.
Phthiracarus affine: Turk, 1953 : 89.

ADULT (Pl. 3a): Small and moderately sclerotized. The *aspis* (Fig. 1C, D) ranges in length from 223 – 253 µm with a greatest width of 162 – 192 µm. All the dorsal setae are fine and short. Setae (*il*) are about 1·5 times the length of setae (*la*) and extend two-thirds of the distance between the bases of setae (*il*) and (*ro*). The latter do not reach the anterior limit of the aspis. The sensillus (Fig. 1B; Pl. 3d) is 50 – 60 µm long, lanceolate and serrated. The *notogaster* (Fig. 1A, E) ranges in length from 406 – 487 µm with a greatest depth of 294 – 345 µm. All the setae are relatively long (equal to the distance $c_1 - d_1$), fine and erect. Setae c_1 and c_3 are inserted on the posterior margin of the collar and seta c_2 submarginally. Vestigial f_1 is located a short distance posterior to seta h_1. The fissures *ip* and *ips* are absent. On each *anal plate* (Fig. 2E) there are three setae; an_1 and an_2 being much longer than ad_3. The *chelicerae* (Fig. 2B, C) are about 121 µm long. The principal segment carries 14 – 26 sharply pointed spines on the paraxial surface and 9 – 21 conical spines antiaxially. The *leg chaetotaxy* (Figs 4; 5) is of the 'complete type' with the setal formulae: I (1–4–2–5–16–1); II (1–3–2–3–12–1); III (2–2–1–2–10–1) and IV (2–1–1–2–10–1). On tarsus I the distal seta coupled with solenidion ω_2 is short; its form can only be seen clearly in scanning electron micrographs (Pl. 2a, b). Seta *u′* on tarsi I and II is often short and thick and resembles a eupathidium. On femur I seta *d* is short, serrated and curved distally (Pl. 2d).

DISTRIBUTION: *P. affinis* is apparently widely distributed in forest soils with a mor humus formation. This species was recorded in the F (fermentation) and H (humus) layers under both the hardwood and coniferous tree species at each of the four study areas (see p. 324) being particularly abundant in the F layer under beech and oak where it constituted 20 – 30 % of the euptyctimoid population. Material collected from the following localities was also examined:

Wytham Woods Estate, Berkshire, 28.x.70 (T. G. Wood); St. Agnes, Isles of Scilly, Cornwall, 5.iv.57 (K. H. Hyatt); Bramshill Forest, Hampshire, 6.xii.70 (B. W. Parry); Woodwalton Fen, Huntingdonshire, 20.v.65 (P. N. Lawrence); Keston Bog, Kent, 8.i.56 (P. N. Lawrence); Thetford Chase, Norfolk, 23.vi.71 (B. W. Parry); Springwell Forest, Co. Londonderry, 1973 (J. Longworth); as well as material labelled '*Hoploderma affine* Hull (Ninebanks)' in the Hull Collection deposited in the BMNH.

REMARKS: Hull (1914) recorded *affinis* in moss in woods and in *Sphagnum* on moors, West Allendale, Northumberland and Gibside, Durham and later (1916) included it in his key to species of the genus *Hoploderma*. A holotype does not appear to have been designated and no type material is known to exist. Hull's collection was found to contain one tube labelled *Hoploderma affine*. Three of the specimens are in good condition, conspecific and the shape of their sensilli corresponds with Hull's description: 'Pseudostigmatic organs prominent, slender, fusiform, curved outward and forward, rather long, with a fine point'. Moreover, the specimens are of a similar size to that given by Hull (about 420 μm). One of these specimens, BMNH reg. no. 1973.28 (now mounted in Berlese's fluid), is hereby designated as the ***neotype***. The fourth specimen, although badly damaged, is clearly another larger species with a differently shaped sensillus. The other British material has been compared with the neotype – no morphological differences apart from size variation could be detected.

P. affinis appears to be close to *P. crenophilus*, a species described by Willmann (1951) from the edge of a marsh, Ebreichsdorf, Austria, and earlier identified as *P. borealis* (Trägårdh) (see Willmann, 1923, 1928 & 1931). The syntype series (10 specimens collected in Austria, Germany and Switzerland) has been examined and found to be composed of two species, only one of which resembles Willmann's figure of *crenophilus* and also the neotype of *P. affinis*. However, the notogastral setae of the latter are considerably shorter than in *P. crenophilus*.

Phthiracarus anonymum Grandjean
(Fig. 6; Pl. 3b, e)

Phthiracarus anonymum Grandjean 1933 : 312 (ano-genital region); 1934 : 51 (aspis & notogaster); 1950 : 73 (setae f_1, f_2 and ps_4); van der Hammen, 1965 : 376 (leg chaetotaxy).
[*Phthiracarus anonymum*: Feider & Suciu, 1957 : 24. Misidentification.]

ADULT (Pl. 3b): Small, weakly sclerotized and opalescent. The *aspis* (Fig. 6C) ranges in length from 208 – 248 μm with a greatest width of 162 – 172 μm. All the dorsal setae are fine and short. Setae (*il*) are about 1·5 times the length of setae (*la*) and extend two-thirds of the distance *il–ro*. The rostrals which are inserted relatively far apart are widely removed from the anterior margin. The sensillus (Fig. 6D) is short (20 μm), ovate and serrated. The *notogaster* (Fig. 6E) ranges in length from 406 – 466 μm with a greatest depth of 253 – 294 μm. All the setae are short (less than the distance $c_1 - d_1$), fine and erect. Setae c_1 and c_3 are inserted on the posterior margin of the collar and seta c_2 submarginally. Vestigial f_1 is located just dorsal to seta h_1. The fissures *ip* and *ips* are absent. On each *anal plate* (Pl. 3e) there are five relatively short setae, of which, three, evidently ad_3 and an_{1-2}, are inserted on the paraxial margin, the longest in the row being an_1 which is approximately twice as long as ad_3. The *chelicerae* are approximately 137 μm in length. The principal segment carries about 12 sharply pointed spines on the paraxial surface and about 10 conical spines antiaxially. The *leg chaetotaxy* is of the 'reduced type' with the setal formulae: I (1–3–2–5–15–1); II (1–3–2–3–11–1); III (2–2–1–2–10–1) and IV (2–1–0–2–8–1). On tarsus I (Fig. 6A) true setae and eupathidia are difficult to distinguish since the former are more or less straight distally. The distal seta coupled with solenidion ω_2 resembles that of *P. affinis*. Seta *u'* on tarsi I and II is often short and thick and resembles a eupathidium. On tarsus IV (Fig. 6B) seta *pv'* is absent.

DISTRIBUTION: *P. anonymum*, the only endophagous species identified in the present study, is apparently widely distributed in the F layer or mor forest soils. This species was common under both the hardwood and coniferous tree species at each of the study areas (see p. 324) being particularly abundant under oak where it constituted 5 – 10% of the euptyctimoid population.

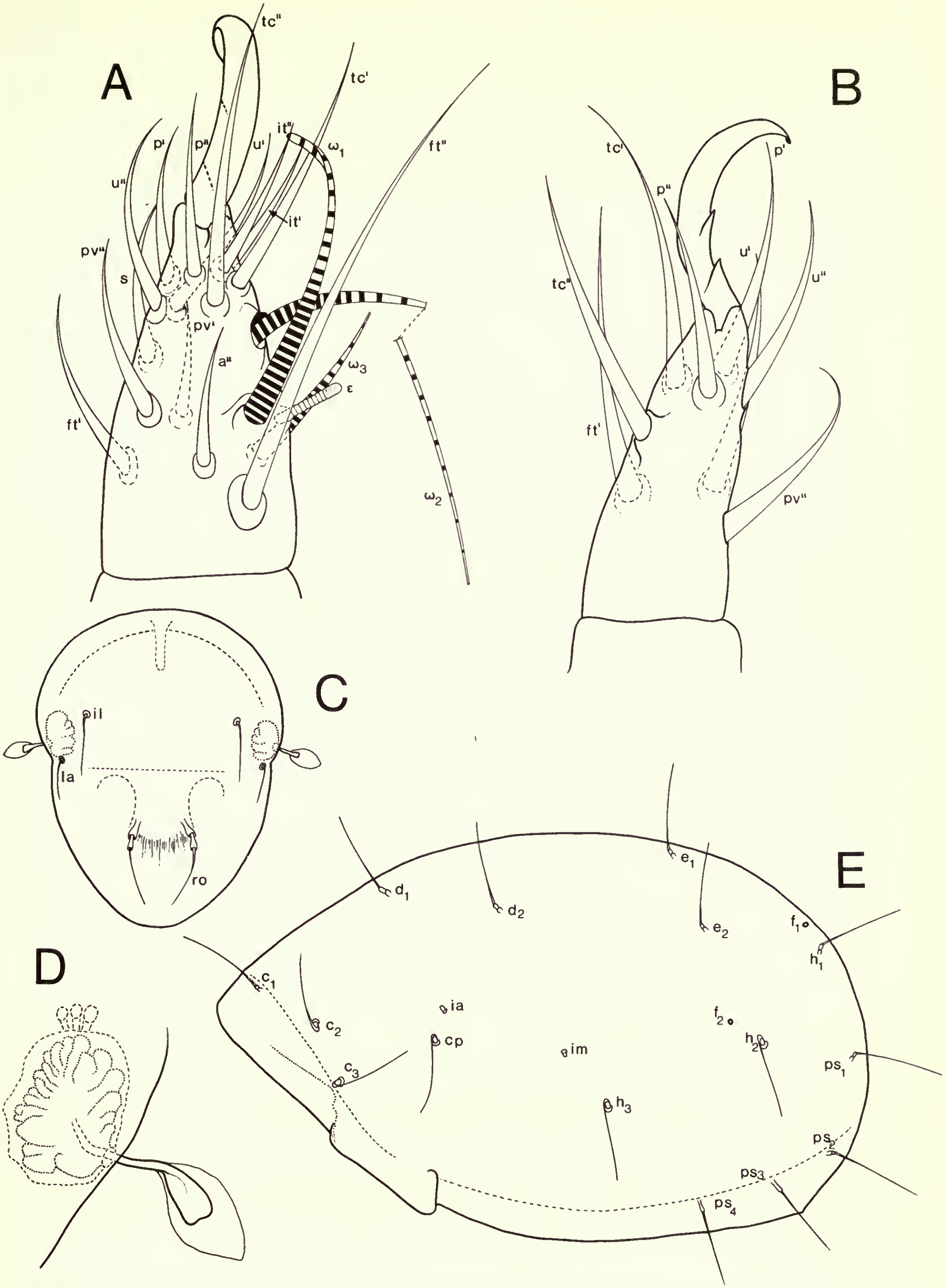
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Fig. 6 *Phthiracarus anonymum*: (A) tarsus I, posterolateral aspect; (B) tarsus IV, posterolateral aspect; (C) aspis, dorsal; (D) sensillus and bothridium; (E) notogaster, lateral. (Fig. 6A, B are drawn at the same magnification.)

Material was also examined from: Wytham Woods Estate, Berkshire, 28.x.70 (T. G. Wood); Burnham Beeches, Buckinghamshire, 1964 (G. O. Evans); Bramshill Forest, Hampshire, 6.xii.70 (B. W. Parry); Woodwalton Fen, Huntingdonshire, 20.iv.65 (P. N. Lawrence); Hollows Wood, Kent, 3.iv.60 (P. N. Lawrence); Grasmere, Westmorland, 3.xii.54 (M. Bacchus); Meathop Wood, Westmorland, 19.iii.63 (P. N. Lawrence); Shawley Woods, Worcestershire, 4.x.63 (F. Flowers); Springwell Forest, Co. Londonderry, 1973 (J. Longworth); Périgueux, Dordogne, France (topotypes).

REMARKS: In comparison with the other British *Phthiracarus* species examined, *P. anonymum* is somewhat atypical: it alone is opalescent; bears f_1 dorsal to h_1; carries ad_3 on the paraxial margin of the anal plate and lacks the anterior primiventral seta on tarsus IV. The British material has been compared with a number of topotypes – no morphological differences could be detected.

P. anonymus amicus Jacot, described from deciduous leaf mould, Connecticut Hill, New York, USA, may well prove to be conspecific with *P. anonymum*. Jacot (1938) based his description on the position of seta d_2 and the length of seta an_1; d_2 was located further towards d_1 than was in fact shown in Grandjean's figure (Grandjean, 1934) while seta an_1 appeared to be longer. Although Grandjean's figure does indeed differ in these two respects from Jacot's *anonymus amicus*, the topotypic material of *anonymum* which has been examined agrees well with Jacot's description. A 'cotype' of *anonymus amicus* (slide no. 32108h2, undissected and mounted in Canada Balsam) has been examined and appears to be close to *anonymum* although the seta an_1 is difficult to discern. Moreover, Jacot's species (diagonal length of notogaster about 400 μm) falls within the size range given by Grandjean (notogastral length 330 – 420 μm).

Phthiracarus clavatus sp. nov.

(Fig. 7A–C; Pl. 3c, f)

ADULT (Pl. 3c): Large and strongly sclerotized. The *aspis* (Fig. 7C) ranges in length from 279 – 324 μm with a greatest width of 192 – 208 μm. All the dorsal setae are long and conspicuous. Setae (*il*) and (*la*) are more or less equal in length and both pairs of setae reach the level of the rostrals. The latter extend to the anterior margin of the aspis. In the paratype setae (*la*) are only half the length of setae (*il*). The sensillus (Fig. 7B; Pl. 3f) is 30 – 40 μm long, broadly clavate and distinctly serrated in the distal half. The *notogaster* (Fig. 7A) ranges in length from 619 – 659 μm with a greatest depth of 421 – 458 μm. All the setae are long (more than the distance $c_1 - d_1$) and procurved. Setae c_{1-3} form a row just behind the posterior margin of the collar. Vestigial f_1 is located a short distance posterior to seta h_1. The fissures *ip* and *ips* are absent. On each *anal plate* there are five long setae; an_{1-2} and ad_3 being more or less equal in length and somewhat shorter than ad_{1-2}. The *chelicerae* are approximately 182 μm in length. The principal segment carries about 20 sharply pointed spines on the paraxial surface and about 18 conical spines antiaxially. The *leg chaetotaxy* is of the 'complete type' with the setal formulae: I (1–4–2–5–16–1); II (1–3–2–3–12–1); III (2–2–1–2–10–1) and IV (2–1–1–2–10–1). On tarsus I the distal seta coupled with solenidion ω_2 is rather short. Seta *d* on femur I is long, straight and only weakly serrated.

TYPES: Holotype, BMNH reg. no. 1976.2.18.1, from mull soil, Meathop Wood, Westmorland, 19.iii.63 (P. N. Lawrence). Paratype, 1976.2.18.2, from *Phragmites* litter, Woodbastwick Marshes, Norfolk, 10.vii.74 (S. J. Moore).

DISTRIBUTION: *P. clavatus* was also recorded from The Woburn Estate, Bedfordshire, 10.iv.72 (B. W. Parry) and from Rosthwaite, Cumberland, 18.v.59 (P. N. Lawrence). This species was not abundant in any of the samples examined.

REMARKS: *P. clavatus* appears to be similar to *P. borealis* (Trägårdh) recorded in rotting birch leaves, Sarek, Swedish Lapland. Three 'cotypes' of *borealis* (cleared but undissected) were examined and found to be generally larger (notogastral length 659 – 842 μm) and more heavily sclerotized than *clavatus*. Moreover, in *P. borealis* the notogastral setae are erect while in *P. clavatus* they are procurved. The general form of the sensillus is similar in both species.

P. clavatus also resembles *P. setosellum bryobium* described by Jacot (1930) from upland

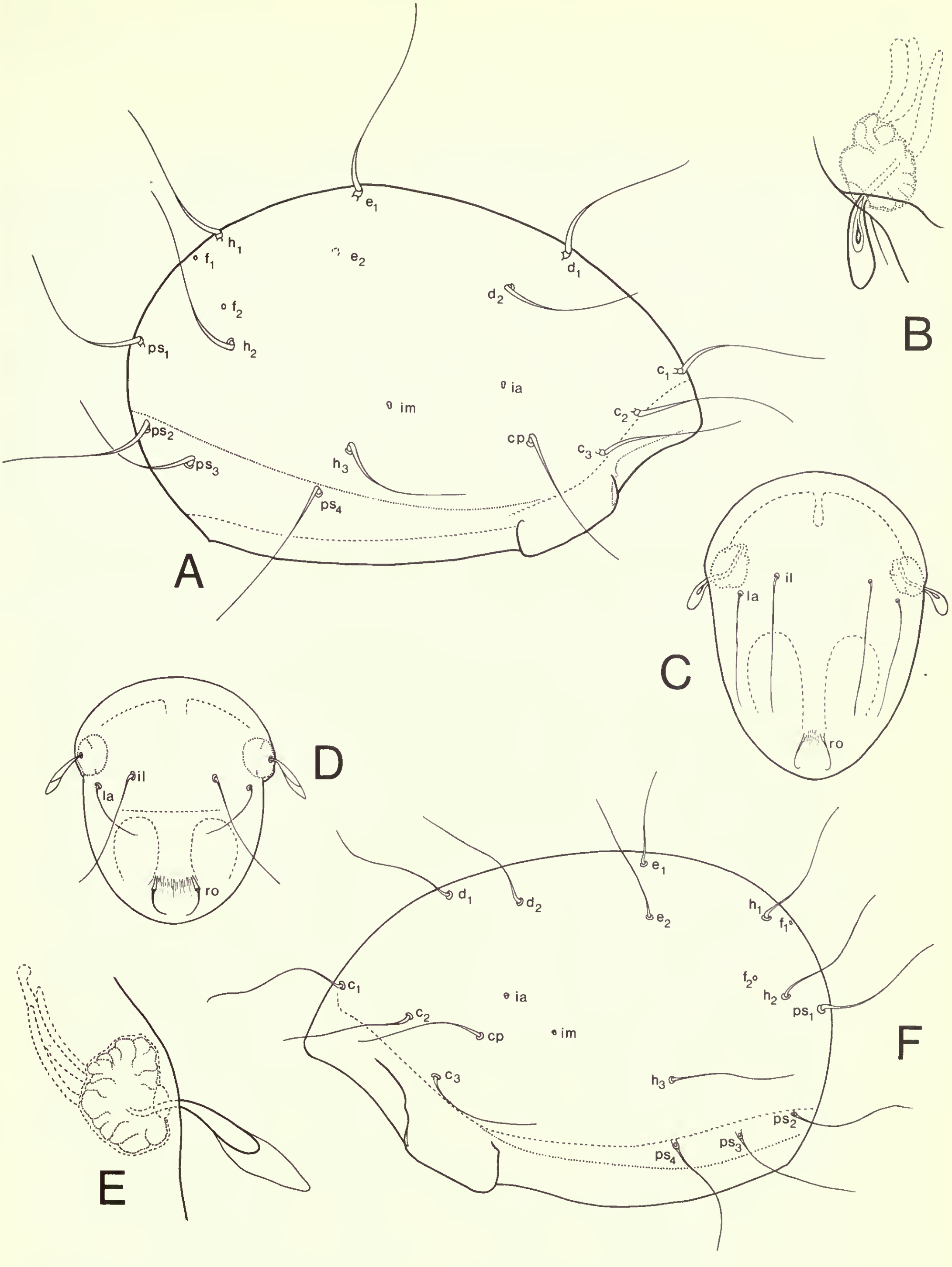
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Fig. 7A–C *Phthiracarus clavatus*: (A) notogaster, lateral; (B) sensillus and bothridium; (C) aspis, dorsal.

Fig. 7D–F *Phthiracarus flexisetosus*: (D) aspis, dorsal; (E) sensillus and bothridium; (F) notogaster, lateral.

swamp moss, East Village, Monroe, Connecticut, USA. However, in comparison with *clavatus*, the 'cotype' of *setosellum bryobium* is much smaller (notogastral length about 252 µm). The notogastral setae appear to be of the same general form in both species. The sensillus, which appears to be lobular in Jacot's figure, is missing in the 'cotype'.

Phthiracarus flexisetosus sp. nov.
(Fig. 7D–F)

ADULT: Medium-sized and moderately strongly sclerotized. The *aspis* (Fig.7D) ranges in length from 230 – 255 µm with a greatest width of 170 – 220 µm. All the dorsal setae are fine and rather long. Setae (*il*) are about 1·5 times the length of setae (*la*) and equal to the distance *il–ro*. The rostrals, which are inserted relatively far apart, do not reach the anterior limit of the aspis. The sensillus (Fig. 7E) is 30 – 40 µm long, broadly clavate, serrated and closely resembles that found in *P. clavatus*. The *notogaster* (Fig. 7F), about 560 µm long and with a greatest depth of about 330 µm, is elongate in lateral aspect. All the setae are long (more than the distance $c_1 - d_1$), fine and slightly flexuose. Setae c_1 and c_3 are inserted on the posterior margin of the collar and seta c_2 submarginally. Vestigial f_1 is located adjacent to seta h_1 and towards the mid-dorsal line. The fissures *ip* and *ips* are absent. On each *anal plate* there are only three setae, of which ad_3 is rather short. The *chelicerae* are about 172 µm long. The principal segment carries 16 – 19 sharply pointed spines on the paraxial surface and 12 – 17 conical spines antiaxially. The *leg chaetotaxy* is of the '*reduced type*' with the setal formulae: I (1–3–2–5–15–1); II (1–3–2–3–11–1); III (2–2–1–2–10–1) and IV (2–1–0–2–9–1). On tarsus I seta *u'* is short, thick and resembles a eupathidium.

TYPES: Holotype, BMNH reg. no. 1976.2.18.17, and two paratypes, 1976.2.18.18–19, from the F layer under a mixed stand of beech and oak, New Forest, Hampshire, 27.iii.73 (B. W. Parry). *P. flexisetosus* is known only from the type locality.

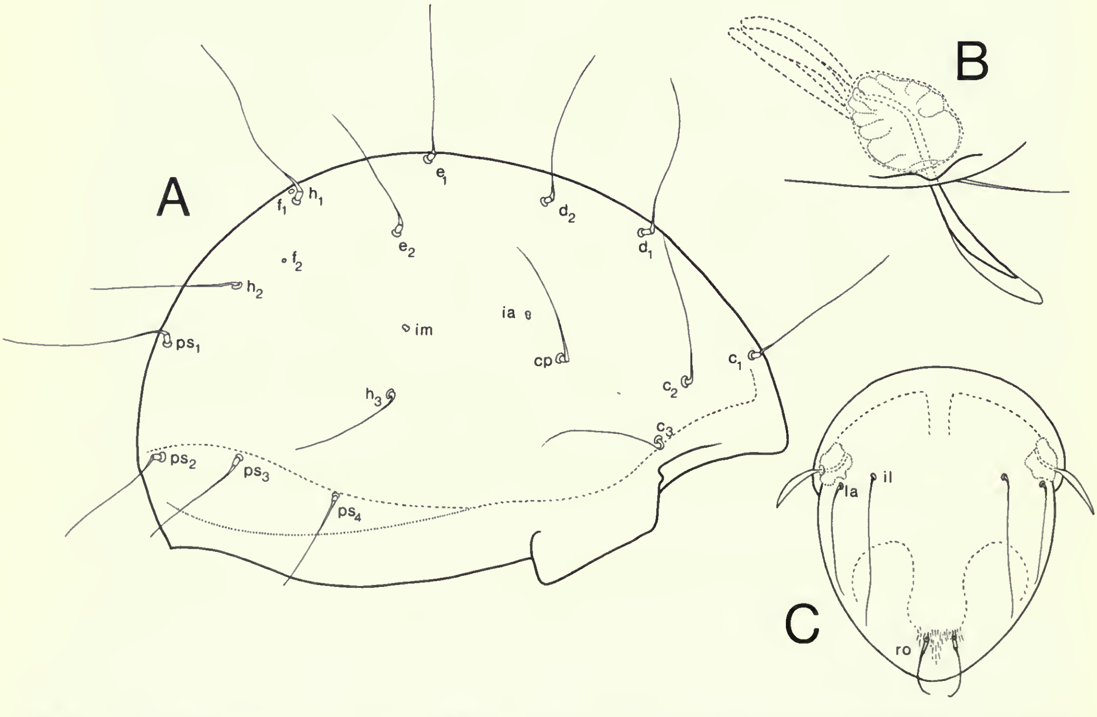

Fig. 8 *Phthiracarus globus*: (A) notogaster, lateral; (B) sensillus and bothridium; (C) aspis, dorsal.

REMARKS: In comparison with the other 'reduced chaetotaxy' species examined, *P. flexisetosus* is rather large and the interlamellar and notogastral setae are much longer.

Phthiracarus globus sp. nov.
(Figs 8; 9; Pl. 4a)

ADULT (Pl. 4a): Large and moderately sclerotized. The *aspis* (Fig. 8C) ranges in length from 324 – 365 µm with a greatest width of 263 – 294 µm. All the dorsal setae are moderately long and fine. Setae (*il*) are about 1·5 times the length of setae (*la*) and almost reach the level of the rostrals. The latter extend beyond the anterior margin of the aspis. The sensillus (Fig. 8B) is 50 – 60 µm long, lanceolate and serrated. It closely resembles that found in *P. affinis*. The *notogaster* (Fig.8A), 578 – 852 µm long and with a greatest depth of 426 – 553 µm, is globular in lateral aspect. All the setae are long (more than the distance $c_1 - d_1$), fine and almost erect. Seta c_3 is inserted on the posterior margin of the collar and setae c_{1-2} submarginally. Vestigial f_1 is located adjacent to seta h_1 and towards the mid-dorsal line. In one paratype f_1 is located a short distance posterior to seta h_1. The fissures *ip* and *ips* are absent. On each *anal plate* there are five long setae; an_{1-2} and ad_3 being more or less equal in length and somewhat shorter than ad_{1-2}. The *chelicerae* are approximately 208 µm long. The principal segment carries about 26 sharply pointed spines on the paraxial surface and about 24 conical spines antiaxially. The *leg chaetotaxy* is of the 'complete type' with the setal formulae: I (1–4–2–5–16–1); II (1–3–2–3–12–1); III (2–2–1–2–10–1) and

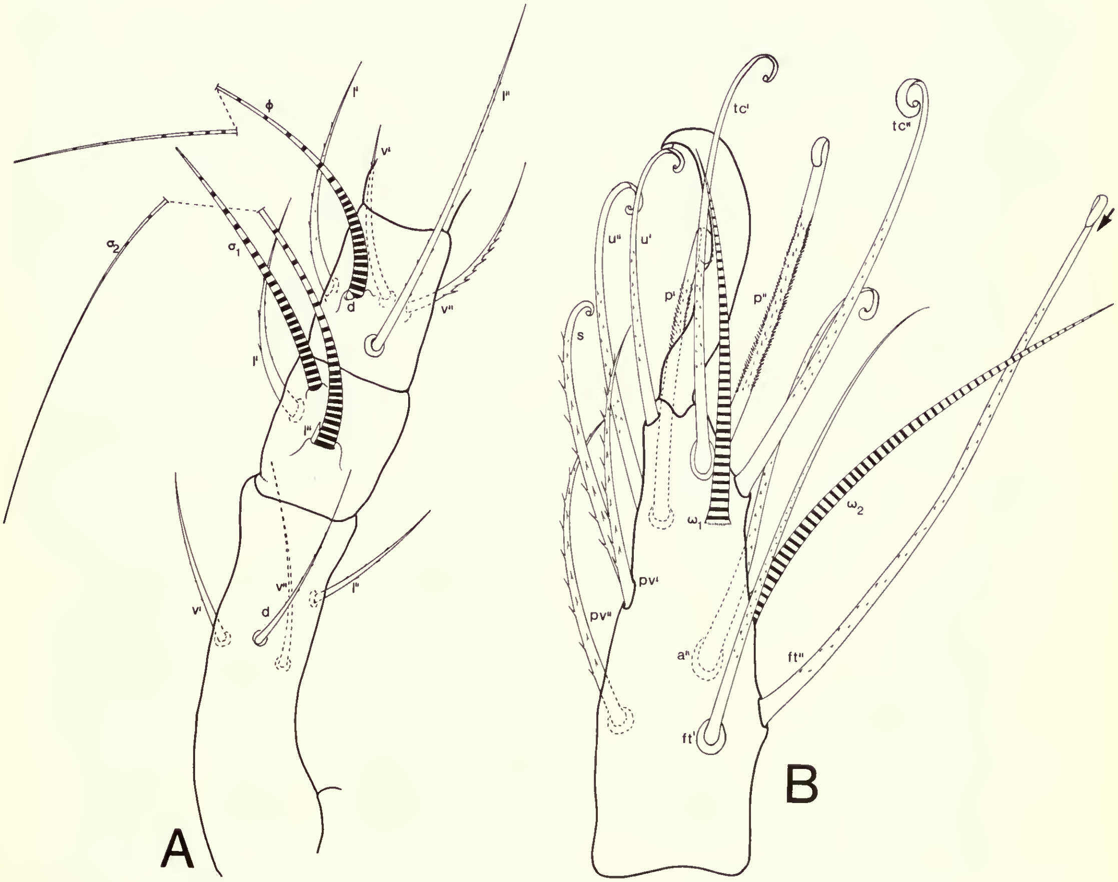

Fig. 9 *Phthiracarus globus*: (A) leg I, trochanter to tibia, dorsal aspect; (B) tarsus II, anterolateral aspect.

IV (2–1–1–2–10–1). Seta *d* on femur I is long, straight and only weakly serrated (Fig. 9A). On tarsus II (Fig. 9B) seta *ft″* is hooked distally.

TYPES: Holotype, BMNH reg. no. 1976.2.18.3, from mosses and liverworts on rocks, Rydal Water, Westmorland, 29.i.54 (P. N. Lawrence). Two paratypes, 1976.2.18.4–5, from mosses, Long Compton Woods, Warwickshire, 15.viii.51 (P. N. Lawrence).

DISTRIBUTION: *P. globus* was also recorded in small numbers in the F and H layers under beech and oak at each of the study areas (see p. 324). Other material was examined from Wytham Woods Estate, Berkshire, 28.ix.70 (T. G. Wood) and from Woodwalton Fen, Huntingdonshire, 20.v.65 (P. N. Lawrence).

REMARKS: Of the 'complete chaetotaxy' species examined, *P. globus* is somewhat unusual in bearing f_1 adjacent to h_1, a feature generally associated with those species having the 'reduced chaetotaxy' combination.

P. globus is similar to *P. clavatus*. However, in contrast to the latter, the sensillus of *P. globus* is lanceolate and the notogastral setae are distinctly procurved. Moreover, in *P. globus* vestigial f_1 is located much closer to the seta h_1.

Phthiracarus juvenalis sp. nov.

(Fig. 10A–C; Pl. 4b, d)

ADULT (Pl. 4b): Medium-sized and weakly sclerotized. The *aspis* (Fig. 10C) ranges in length from 258 – 279 μm with a greatest width of 213 – 223 μm. All the dorsal setae are moderately long and fine. Setae (*il*) are about 1·5 times the length of setae (*la*) and equal to the distance *il–ro*. The latter do not reach the anterior margin of the aspis. The sensillus (Fig. 10B; Pl. 4d) is rather long (80 μm), narrow and pointed distally. The tracheoles are short and finger-like. The *notogaster* (Fig. 10A) ranges in length from 558 – 588 μm with a greatest depth of 365 – 406 μm. All the setae are short (less than the distance $c_1 - d_1$), fine and directed posteriorly. Setae c_1 and c_3 are inserted close to the posterior margin of the collar and seta c_2 submarginally. Vestigial f_1 is located a short distance posterior to seta h_1. The fissures *ip* and *ips* are absent. On each *anal plate* there are two setae in the anal series and one in the adanal series; all are moderately long and more or less equal in length. The *chelicerae* are approximately 152 μm long. The principal segment carries about 19 sharply pointed spines on the paraxial surface and about 15 conical spines antiaxially. The *leg chaetotaxy* is of the 'complete type' with the setal formulae: I (1–4–2–5–16–1); II (1–3–2–3–12–1); III (2–2–1–2–10–1) and IV (2–1–1–2–10–1).

TYPES: Holotype, BMNH reg. no. 1976.2.18.6, and one paratype, 1976.2.18.7, from leaf litter, Higher Kiln Quarry, Buckfastleigh, Devon, 25.iv.64 (C. Moreby).

DISTRIBUTION: Common in mor forest soils. *P. juvenalis* was recorded under both the hardwood and coniferous tree species at each of the study areas (see p. 324) being particularly abundant in beech and oak F where it accounted for 5 – 15% of the euptyctimoid population. Other material was examined from Woodwalton Fen, Huntingdonshire, 20.v.65 (P. N. Lawrence) and from Castor Hanglands, Northamptonshire, 21.vi.63 (P. N. Lawrence).

REMARKS: Of the species examined with a 'complete chaetotaxy', *P. juvenalis* is the only one to possess a rather long sensillus and backwardly directed notogastral setae.

P. ligneus, recorded by Willmann (1932) in humus, moist *Juncus* and moss on the Dummersdorf bank, River Trave, West Germany, shows an overall similarity to *P. juvenalis*. The syntype series (five specimens mounted in Canada Balsam) has been examined, and in comparison to *P. juvenalis* the specimens found to be much smaller (notogastral length 375 – 420 μm) while the notogastral setae and the sensilli are distinctly longer than in *P. juvenalis*.

P. juvenalis also resembles two recently described species, *P. clemens* Aoki 1963 from Tokyo and *P. crispus* Hammer 1972 from Tahiti. However, in comparison with *P. juvenalis*, topotypes of *P. clemens* were found to be larger (notogastral length about 700 μm) while the holotype of *P. crispus* was much smaller (notogastral length about 430 μm). Moreover, in contrast to *P. juvenalis*, the notogastral setae of both species are procurved.

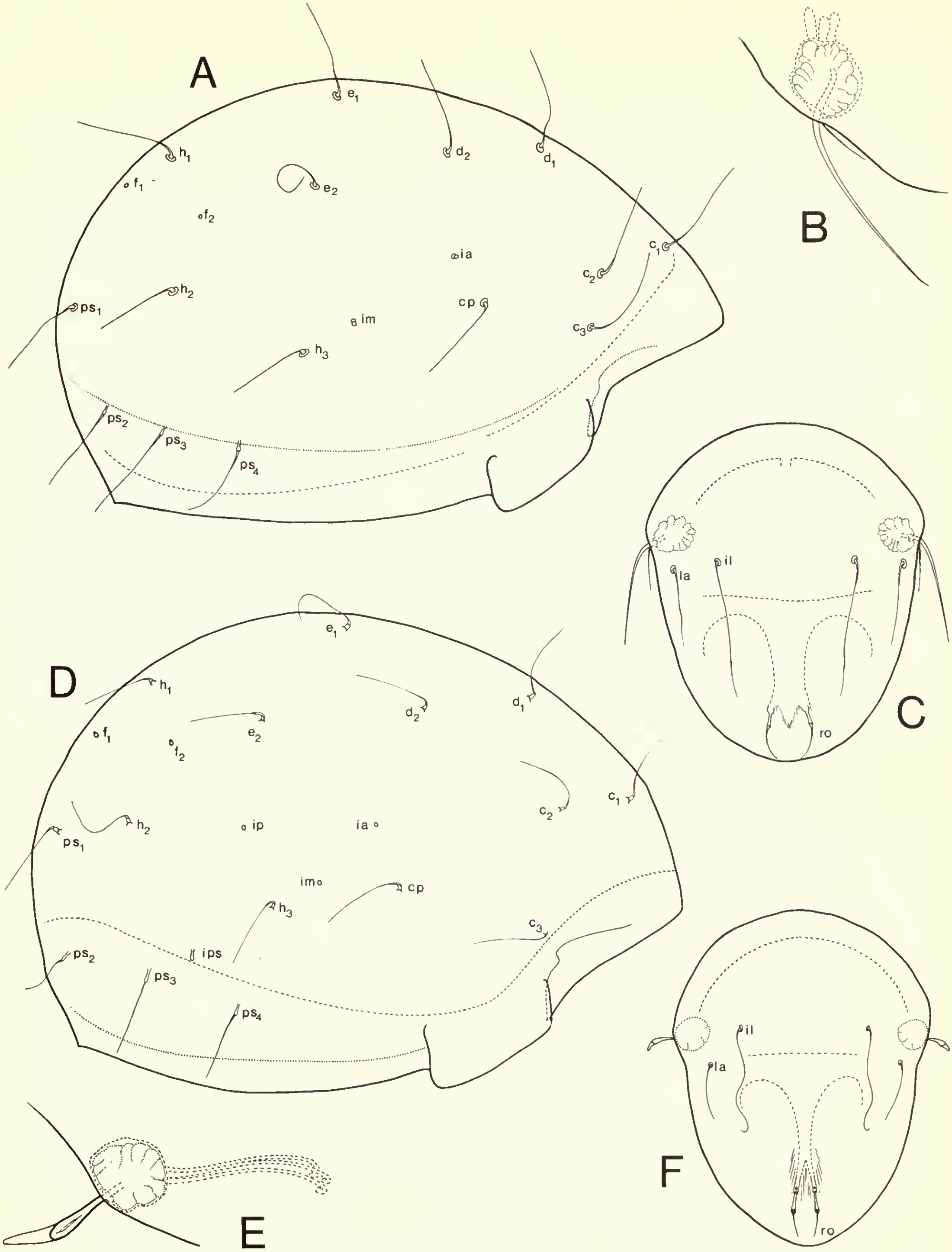
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Fig. 10A–C *Phthiracarus juvenalis*: (A) notogaster, lateral; (B) sensillus and bothridium; (C) aspis, dorsal.

Fig. 10D–F *Phthiracarus laevigatus*: (D) notogaster, lateral; (E) sensillus and bothridium; (F) aspis, dorsal.

Phthiracarus laevigatus (C. L. Koch)
(Fig. 10D–F; Pl. 4e)

Hoplophora laevigata Koch, 1841 : Fasc. 38 t.16; 1842 : 116.
Phthiracarus laevigatus: Jacot, 1936 : 167; van der Hammen, 1963 : 704 (neotype designated).

ADULT: Large and strongly sclerotized. The *aspis* (Fig. 10F) ranges in length from 406 – 456 μm with a greatest width of 355 – 400 μm. All the dorsal setae are fine and short. Setae (*il*) are about 1·5 times the length of setae (*la*) and extend two-thirds of the distance *il–ro*. The sensillus (Fig. 10E) is about 50 μm long, narrow and finely serrated. The *notogaster* (Fig. 10D) ranges in length from 812 – 1065 μm with a greatest depth of 521 – 771 μm, and in lateral view is seen to be sharply angled at the level of seta c_1 (Pl. 4e). The latter is inserted relatively far back. All the setae are short (less than the distance $c_1 - d_1$), fine and procurved. Vestigial f_1 is located midway between setae h_1 and ps_1. The fissures *ip* and *ips* are present. On each *anal plate* there are only three setae, an_{1-2} being much longer than ad_3. The *leg chaetotaxy* is of the 'complete type' with the setal formulae: I(1–4–2–5–16–1); II(1–3–2–3–12–1); III(2–2–1–2–10–1) and IV(2–1–1–2–10–1).

DISTRIBUTION: Three specimens only have been recorded in the British Isles from beech litter, Old Winchester Hill, Hampshire, 1971 (D. R. Kime).

REMARKS: *P. laevigatus* is quite distinctive, being easily recognized by the marked angle of the notogaster at the level of seta c_1. The leg chaetotaxy is similar to that noted for the other 'complete chaetotaxy' species; on tarsus I the solenidion ω_2 is coupled with a small distal seta, a feature not mentioned by van der Hammen in his redescription. The British material has been compared with the neotype from Regensburg – no morphological differences could be detected.

P. brevisetae Jacot, described from decaying grass, Monroe, Connecticut, USA, appears to be close to *P. laevigatus*. The holotype (slide no. 2534h) has been examined and found to be badly damaged. Jacot's description (Jacot, 1930), however, agrees well with van der Hammen's (1963) and with the British material, but the attitude of the notogastral setae appears to differ slightly. In *P. laevigatus* the notogastral setae are procurved while in *P. brevisetae* they are directed posteriorly.

Phthiracarus membranifer sp. nov.
(Fig. 11A–C)

ADULT: Small and weakly sclerotized. The *aspis* (Fig. 11C) ranges in length from 213 – 324 μm with a greatest width of 157 – 243 μm. All the dorsal setae are fine and short. Setae (*il*) are about 1·5 times the length of setae (*la*) and extend two-thirds of the distance *il–ro*. The latter do not reach the anterior limit of the aspis. The sensillus (Fig. 11B) is 70 μm long, narrow, membranous marginally and reminiscent of that of *P. juvenalis*. The tracheoles are short and finger-like. The *notogaster* (Fig. 11A) ranges in length from 314 – 517 μm with a greatest depth of 223 – 324 μm. All the setae are relatively long (equal to the distance $c_1 - d_1$), fine and almost erect. Setae c_1 and c_3 are situated on the posterior margin of the collar and just anterior to seta c_2. Vestigial f_1 is located a short distance posterior to seta h_1. The fissures *ip* and *ips* are absent. On each *anal plate* there are only three setae; an_{1-2} being much longer than ad_3. The *chelicerae* are 116 – 167 μm long. The principal segment carries 9 – 23 sharply pointed spines on the paraxial surface and 8 – 20 conical spines antiaxially. The *leg chaetotaxy* is of the 'reduced type' with the setal formulae: I (1–3–2–5–15–1); II (1–3–2–3–11–1); III (2–2–1–2–10–1) and IV (2–1–0–2–9–1). On tarsus I seta *u′* is short, thick and resembles a eupathidium. In one paratype the 'complete chaetotaxy' condition of tarsi I to IV (16, 12, 10 and 10) is associated with a 'reduced chaetotaxy' condition on femur I (3) and genu IV (0).

TYPES: Holotype, BMNH reg. no. 1976.2.18.14, and two paratypes, 1976.2.18.15–16, from Sitka spruce F, Tintern Forest, Monmouthshire, 4.vi.73 (B. W. Parry).

DISTRIBUTION: *P. membranifer* was also recorded from Higher Kiln Quarry, Devon, 25.iv.64 (C. Moreby) and from Torboll, Sutherland, 29.vi.76 (P. D. Hillyard). This species was not abundant in any of the samples examined.

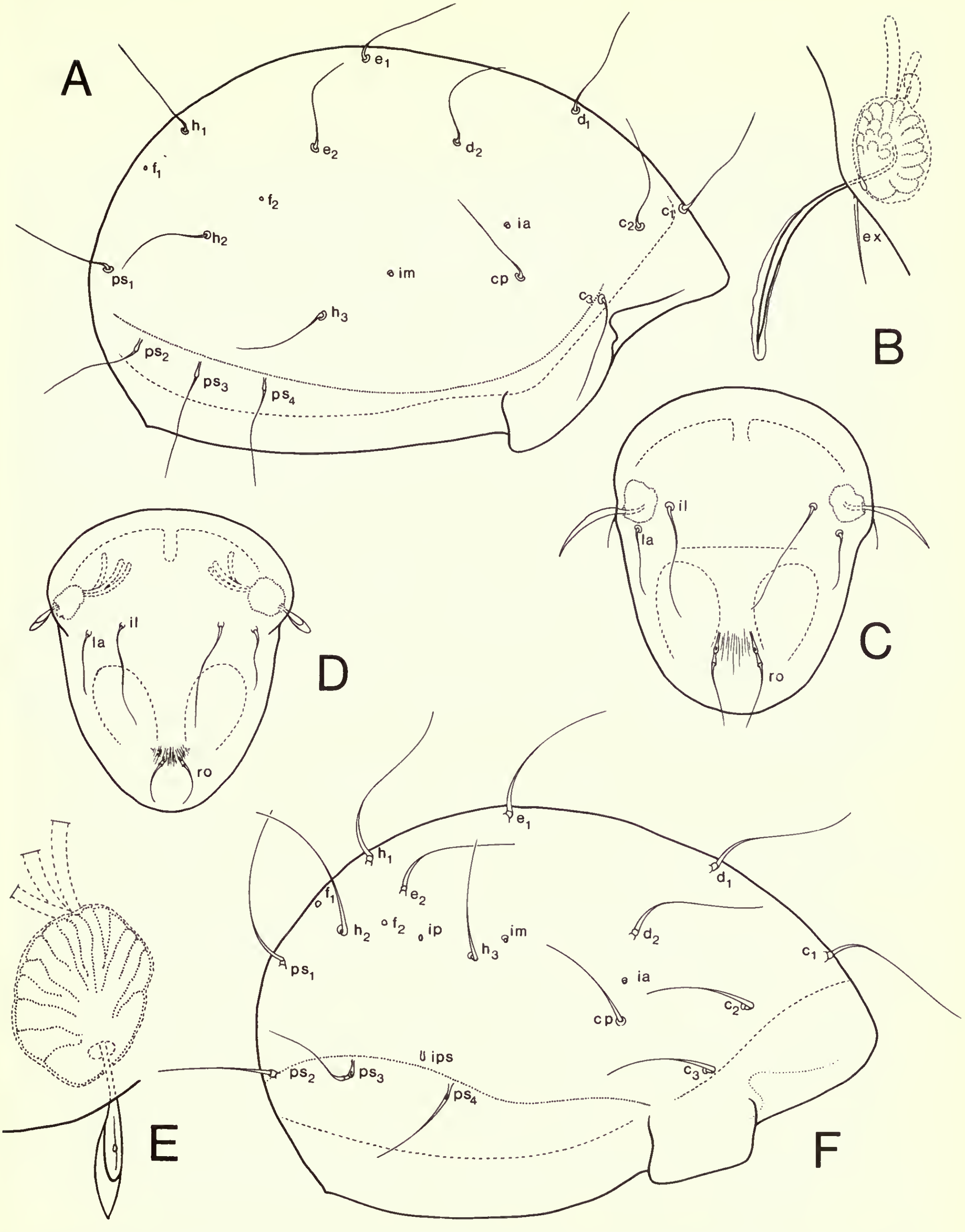
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Fig. 11A–C *Phthiracarus membranifer*: (A) notogaster, lateral; (B) sensillus and bothridium; (C) aspis, dorsal.

Fig. 11D–F *Phthiracarus murphyi*: (D) aspis, dorsal; (E) sensillus and bothridium; (F) notogaster, lateral.

REMARKS: The smallest of the British species examined, *P. membranifer* is somewhat unusual in bearing vestigial f_1 posterior to the seta h_1 (a feature generally associated with the larger 'complete chaetotaxy' species).

Phthiracarus murphyi Harding
(Fig. 11D–F; Pl. 4c)

Phthiracarus murphyi Harding, 1976 : 164.

ADULT (Pl. 4c): Large and strongly sclerotized. The *aspis* (Fig. 11D) is about 300 µm in length with a greatest width of about 250 µm. All the dorsal setae are fine and short. Setae (*il*) are about 1·5 times the length of setae (*la*) and extend two-thirds of the distance *il–ro*. Setae (*ro*) do not reach the anterior limit of the aspis. The sensillus (Fig. 11E) is short (40 – 50 µm), ovate and serrated. The *notogaster* (Fig. 11F) is about 700 µm in length with a greatest depth of about 420 µm. All the setae are relatively long (equal to the distance $c_1 - d_1$) and markedly procurved. Seta c_3 is inserted on the posterior collar margin and setae c_{1-2} submarginally. Vestigial f_1 is located midway between setae h_1 and ps_1. The fissures *ip* and *ips* are present. On each *anal plate* there are five long setae; an_{1-2} and ad_3 being more or less equal in length and somewhat shorter than ad_{1-2}. The *chelicerae* are approximately 213 µm in length. The principal segment carries about 18 sharply pointed spines on the paraxial surface and about 16 conical spines antiaxially. The *leg chaetotaxy* is of the 'complete type' with the setal formulae: I (1–4–2–5–16–1); II (1–3–2–3–12–1); III (2–2–1–2–10–1) and IV (2–1–1–2–10–1). On tarsus I the distal seta coupled with solenidion ω_2 is rather short. Seta *ft″* on tarsus II is hooked distally.

DISTRIBUTION: This species was collected in small numbers from Wytham Woods Estate, Berkshire, 28.x.70 (T. G. Wood) and from Torboll, Sutherland, 29.vi.76 (P. D. Hillyard).

REMARKS: Although rather larger, *P. murphyi* appears to bear some resemblance to *P. insularis* Jacot (notogastral length about 500 µm) recorded from Teuanui, Tovii, the Marquesas Islands. Jacot (1935) did not refer in his description to the fissures *ip* and *ips* although his figure shows quite clearly that these fissures are present. In comparison with *P. murphyi*, the notogastral setae of *insularis* appear to be shorter (less than the distance $c_1 - d_1$). Unfortunately, the 'cotype' of *P. insularis* is apparently lost.

Phthiracarus nitens (Nicolet)
(Fig. 12A–C)

Hoplophora nitens Nicolet, 1855 : 472.
Phthiracarus nitens: van der Hammen, 1964 : 400 (neotype designated).

ADULT: Large and moderately sclerotized. The *aspis* (Fig. 12B) ranges in length from 253 – 460 µm with a greatest width of 213 – 360 µm. All the dorsal setae are fine and short. Setae (*il*) are about 1·5 times the length of setae (*la*) and extend two-thirds of the distance *il–ro*. The sensillus (Fig. 12A) is 50 – 60 µm in length, narrow and resembles that of *P. laevigatus*. The *notogaster* (Fig. 12C) ranges in length from 502 – 900 µm with a greatest depth of 299 – 600 µm. All the setae are short (less than the distance $c_1 - d_1$), fine and procurved. Seta c_3 is inserted on the posterior margin of the collar and setae c_{1-2} submarginally. Vestigial f_1 is located midway between setae h_1 and ps_1. The fissures *ip* and *ips* are present. On each *anal plate* there are only three setae; an_{1-2} being much longer than ad_3. The *chelicerae* are approximately 270 µm long. The principal segment carries 17 – 21 sharply pointed spines on the paraxial surface and 10 – 19 conical spines antiaxially. The *leg chaetotaxy* is of the 'complete type' with the setal formulae: I (1–4–2–5–16–1); II (1–3–2–3–12–1); III (2–2–1–2–10–1) and IV (2–1–1–2–10–1). On tarsus II seta *ft″* is hooked distally.

DISTRIBUTION: *P. nitens* was collected in small numbers from the following localities: Wytham Woods Estate, Berkshire, 28.x.70 (T. G. Wood); St Agnes, Isles of Scilly, Cornwall, 5.iv.57 (K. H. Hyatt); Higher Kiln Quarry, Devon, 25.iv.64 (C. Moreby); Tring Deer Park, Hertfordshire, 1.ii.64 (P. N. Lawrence).

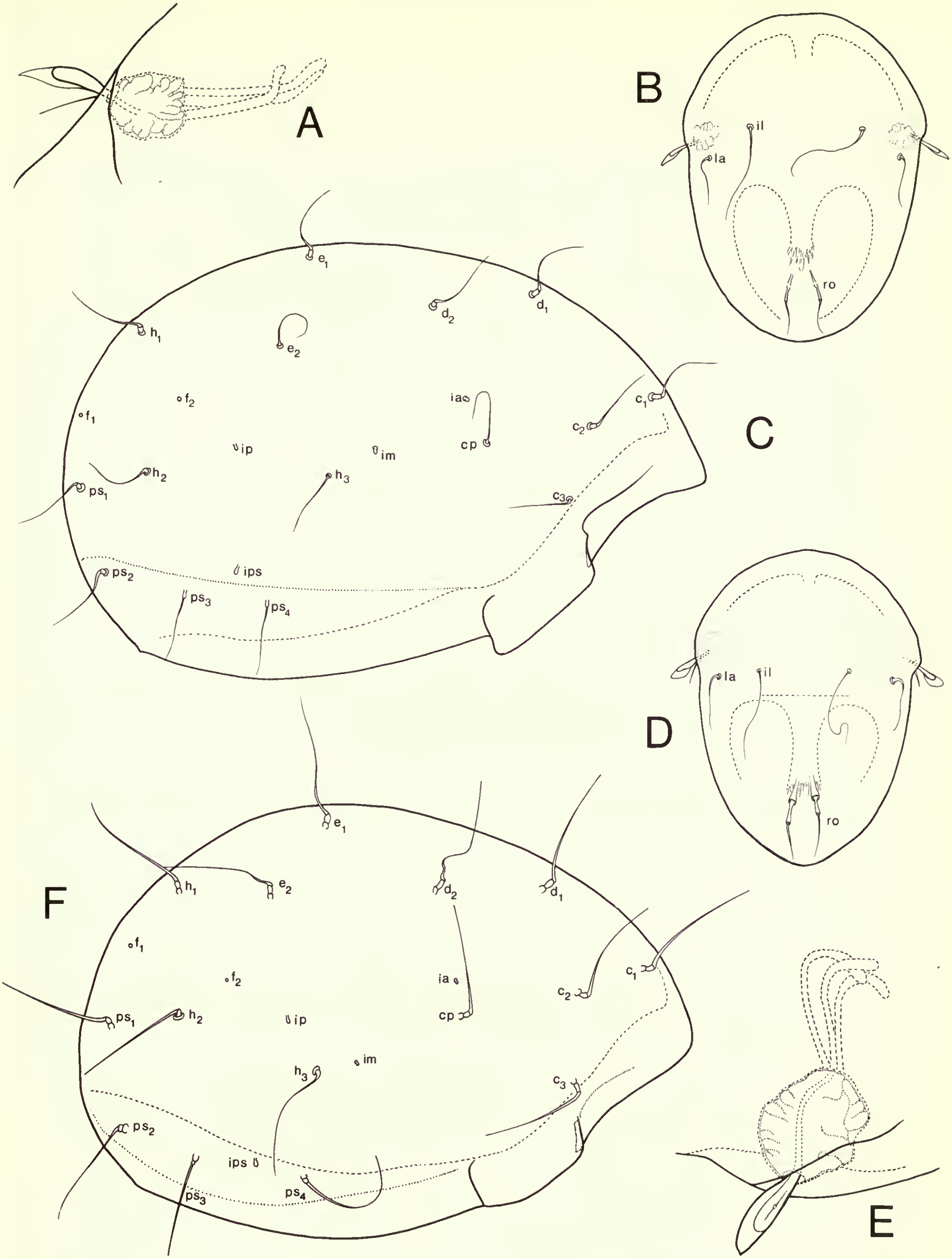
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Fig. 12A–C *Phthiracarus nitens*: (A) sensillus and bothridium; (B) aspis, dorsal; (C) notogaster, lateral.

Fig. 12D–F *Phthiracarus rectisetosus*: (D) aspis, dorsal; (E) sensillus and bothridium; (F) notogaster, lateral.

REMARKS: The neotype from Regensburg has been examined and in comparison with the British material the notogastral setae appear to be somewhat longer. The leg chaetotaxy is of the 'complete type'. On tarsus I the solenidion ω_2 is coupled with a short distal seta and on tarus II the posterior fastigial seta is hooked distally. Neither of these features was noted by van der Hammen in his redescription.

P. nitens is similar to if not conspecific with *P. montanus* recorded by Pérez-Iñigo in grassland soil and moist moss, Sierra de Guadarrama, Spain. The holotype was examined and seen to be cleared but undissected. In comparison with *P. nitens*, it differs only in the form of the distal region of the sensillus which is lobular in *montanus* and pointed in *nitens*.

Phthiracarus rectisetosus sp. nov.

(Fig. 12D–F; Pl. 5c)

ADULT (Pl. 5c): Large and strongly sclerotized. The *aspis* (Fig. 12D) ranges in length from 350 – 477 µm with a greatest width of 268 – 360 µm. All the dorsal setae are fine and short. Setae (*il*) which are inserted rather far forward and on a level with setae (*la*) are about 1·5 times the length of the latter and extend two-thirds of the distance *il–ro*. Setae (*ro*) do not reach the anterior limit of the aspis. The sensillus (Fig. 12E) is 40 µm long, ovate, serrated distally and resembles that found in *P. murphyi*. The *notogaster* (Fig. 12F) ranges in length from 710 – 994 µm with a greatest depth of 482 – 720 µm. All the setae are relatively long (equal to the distance $c_1 - d_1$) and almost erect. Setae c_1 and c_3 are situated on the posterior margin of the collar and seta c_2 submarginally. Vestigial f_1 is located a short distance posterior to seta h_1. The fissures *ip* and *ips* are present. On each *anal plate* there are five long setae; an_{1-2} and ad_3 being more or less equal in length and somewhat shorter than ad_{1-2}. The *chelicerae* are 168 – 294 µm long. The principal segment carries 22 – 24 sharply pointed spines on the paraxial surface and 17 – 22 conical spines antiaxially. The *leg chaetotaxy* is of the 'complete type' with the setal formulae: I (1–4–2–5–16–1); II (1–3–2–3–12–1); III (2–2–1–2–10–1) and IV (2–1–1–2–10–1). On tarsus I the distal seta coupled with solenidion ω_2 is almost as long as the famulus. Seta *ft"* on tarsus II is hooked distally.

TYPES: HOLOTYPE, BMNH reg. no. 1976.2.18.8, and one paratype, 1976.2.18.9, from beech litter, Burnham Beeches, Buckinghamshire, 1964 (G. O. Evans). Two paratypes, 1976.2.18.10–11, from beech F, Wytham Woods Estate, Berkshire, 28.ix.70 (T. G. Wood).

DISTRIBUTION: Common in mor soils particularly under beech. *P. rectisetosus* is evidently widely distributed in the British Isles and was abundant in all the samples examined from Monks Wood, Cambridgeshire, 16.v.75 (J. A. Moffat); Woodbastwick Marshes, Norfolk, 10.vii.74 (S. J. Moore); West Allendale, Northumberland, 18.ix.75 (R. M. Emberson); Long Compton Woods, Warwickshire, 15.viii.51 (P. N. Lawrence); Hag Wood, Yorkshire, 12.iv.71 (D. R. Kime); Newtonmore, Inverness-shire, 3.vii.73 (M. J. Bishop); Lochdonhead and Tobermory, Mull, 28.v.70 (P. N. Lawrence); Torboll, Sutherland, 29.vi.76 (P. D. Hillyard); Llanthony, Monmouthshire, i.iv.73 (M. J. Bishop).

REMARKS: *P. rectisetosus* bears some resemblance to two other 'complete chaetotaxy' species, namely *P. clavatus* and *P. globus*. However, *P. rectisetosus* bears four pairs of lateral fissures while *P. clavatus* and *P. globus* bear only two pairs.

Phthiracarus serrulatus sp. nov.

(Fig. 13A–C; Pl. 5b)

ADULT (Pl. 5b): Small and weakly sclerotized. The *aspis* (Fig. 13C) ranges in length from 182 – 213 µm with a greatest width of 137 – 157 µm. All the dorsal setae are fine and short. Setae (*il*) are about 1·5 times the length of setae (*la*) and extend two-thirds of the distance *il–ro*. The rostrals which are inserted relatively far apart do not reach the anterior limit of the aspis. The sensillus (Fig. 13B) is long (70 µm), narrow and tapers to a point distally with three or four straight-edged teeth subterminally. The tracheoles are short and finger-like. The *notogaster* (Fig. 13A) ranges in length from 456 – 466 µm with a greatest depth of 324 – 334 µm. All the

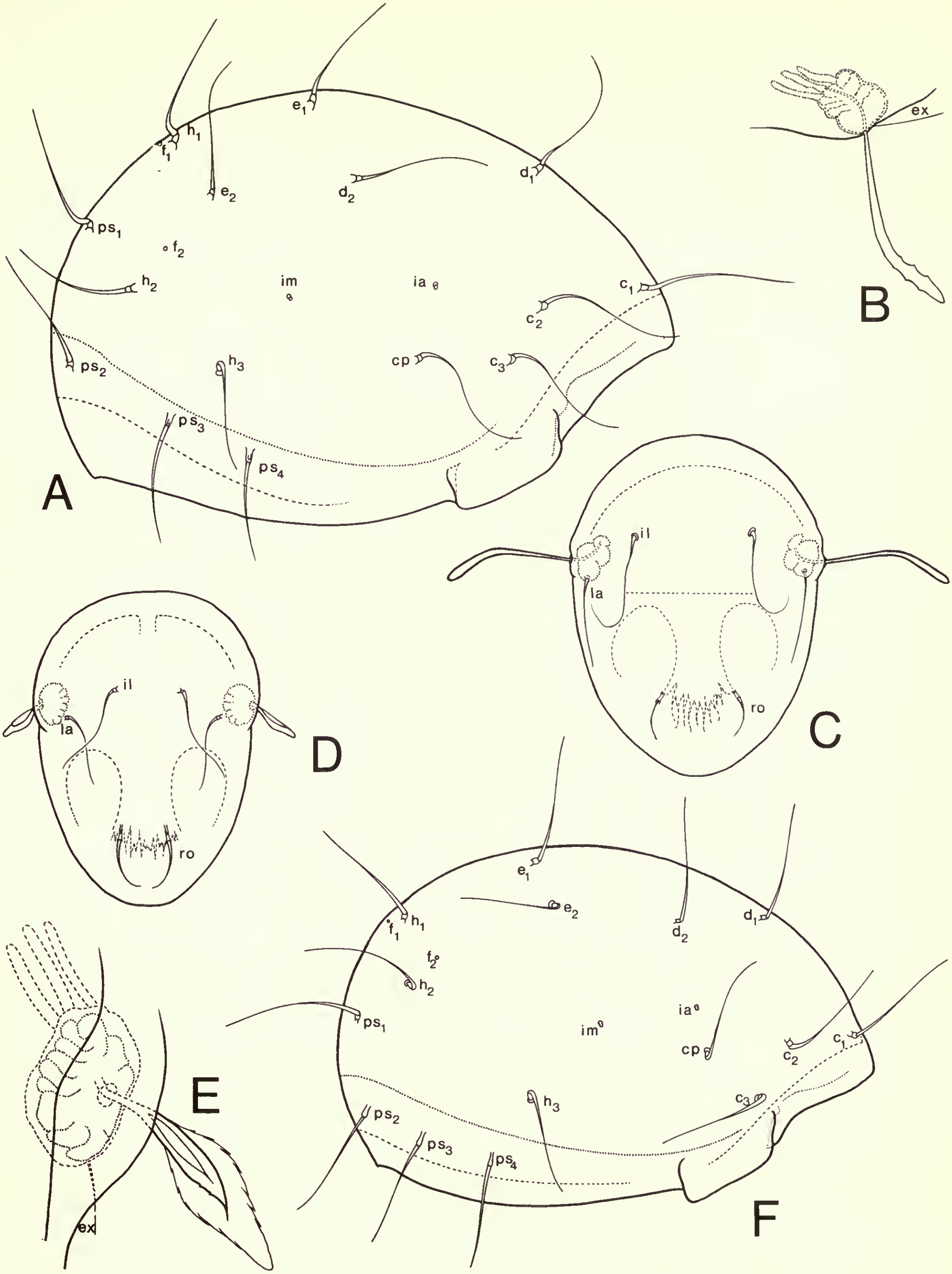
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Fig. 13A–C *Phthiracarus serrulatus*: (A) notogaster, lateral; (B) sensillus and bothridium; (C) aspis, dorsal.

Fig. 13D–F *Phthiracarus tardus*: (D) aspis, dorsal; (E) sensillus and bothridium; (F) notogaster, lateral.

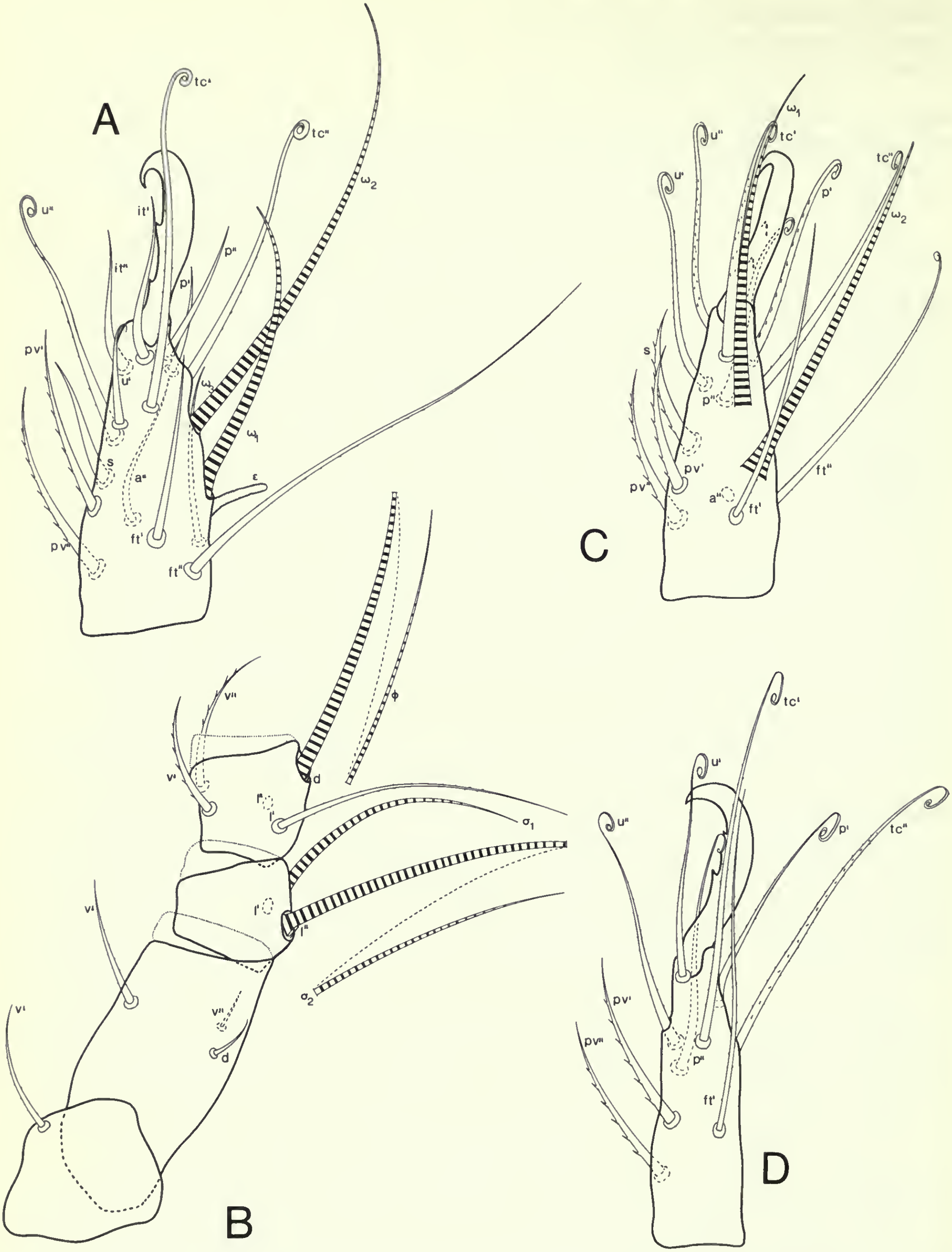
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Fig. 14 *Phthiracarus tardus*, anterolateral aspect of legs I, II and IV: (A) tarsus I; (B) leg I, trochanter to tibia; (C) tarsus II; (D) tarsus IV. (Fig. 14A–D are drawn at the same magnification.)

setae are relatively long (equal to the distance $c_1 - d_1$), fine and procurved. Seta c_1 is inserted on the posterior collar margin and setae c_{2-3} submarginally. Vestigial f_1 is located adjacent to seta h_1 and towards the mid-dorsal line. The fissures *ip* and *ips* are absent. On each *anal plate* there are two setae in the anal series and one in the adanal series – all are moderately long and more or less equal in length. The *chelicerae* are approximately 120 µm long. The principal segment carries about 17 sharply pointed spines on the paraxial surface and about 16 conical spines antiaxially. The *leg chaetotaxy* is of the 'reduced type' with the setal formulae: I (1–3–2–5–15–1); II (1–3–2–3–11–1); III (2–2–1–2–10–1) and IV (2–1–0–2–9–1).

TYPES: Holotype, BMNH reg. no. 1976.2.18.12, and one paratype, 1976.2.18.13, from beech F, Wytham Woods Estate, Berkshire, 28.ix.70 (T. G. Wood). *P. serrulatus* is only known from the type locality.

REMARKS: *P. serrulatus* shows an overall similarity to *P. minimarginatus* Woolley 1954, a species described from Colorado, USA. However, in comparison with *serrulatus*, the holotype of *minimarginatus* (dissected, partially cleared and mounted in Berlese's fluid) was found to possess shorter notogastral setae while vestigial f_1 was located midway between setae h_1 and ps_1. Moreover, the sensillus of the American species was found to bear many more distal serrations than that of *P. serrulatus*. Both species are of a similar size (about 450 µm).

Phthiracarus tardus Forsslund
(Figs 13D–F; 14; Pl. 5a, d)

Phthiracarus tardus Forsslund, 1956 : 216.

ADULT (Pl. 5a): Small and weakly sclerotized. The *aspis* (Fig. 13D) is about 223 µm in length with a greatest width of about 187 µm. All the dorsal setae are fine and short. Setae (*il*) are about 1·5 times the length of setae (*la*) and extend two-thirds of the distance *il–ro*. The rostrals which are inserted relatively far apart do not reach the anterior limit of the aspis. The sensillus (Fig. 13E; Pl. 5d) is 30 – 40 µm in length and broadly clavate. The *notogaster* (Fig. 13F) is about 497 µm in length with a greatest depth of about 314 µm. All the setae are relatively long (equal to the distance $c_1 - d_1$), fine and erect. Setae c_{1-3} form a row just behind the posterior margin of the collar. Vestigial f_1 is located adjacent to seta h_1 and towards the mid-dorsal line. The fissures *ip* and *ips* are absent. On each *anal plate* there are only three setae; an_{1-2} being much longer than ad_3. The *chelicerae* are approximately 147 µm long. The principal segment carries about 16 sharply pointed spines on the paraxial surface and about 9 conical spines antiaxially. The *leg chaetotaxy* (Fig. 14) is of the 'reduced type' with the setal formulae: I (1–3–2–5–15–1): II (1–3–2–3–12–1); III (2–2–1–2–10–1) and IV (2–1–0–2–9–1). On tarsus I seta *u'* is short, thick and resembles a eupathidium. Seta *ft''* on tarsus II is hooked distally and this segment carries a subunguinial seta *s*.

DISTRIBUTION: Only a small number of specimens have been recorded in the British Isles from mull soil, Meathop Wood, Westmorland, 19.iii.63 (P. N. Lawrence).

REMARKS: *P. tardus* is somewhat unusual in bearing 12 setae on tarsus II and by having a hooked posterior fastigial seta on this segment (both features are generally associated with 'complete chaetotaxy' species).

A comparison of British and paratype material revealed no morphological differences.

'Complete' and 'reduced' leg chaetotaxy – a possible basis for a subdivision of the genus *Phthiracarus*

The earliest proposed subdivision of the genus *Phthiracarus* appears to be that of Feider and Suciu (1957) who recognized two species groups based solely on the shape of the sensillus. Their '*anonymum* group' included species with spindle-shaped sensilli (*anonymum*, *globosus*, *lanatus* and *piger*) and their '*lentulus* group' species with thread-like sensilli (*baloghi*, *italicus*, *lentulus*, *ligneus*, *parabotrichus* and *sellnicki*). However, these do not appear to be satisfactory groupings since the present study has suggested that sensillar shape is not correlated with other features, such as the chaetotactic pattern of the legs or notogaster.

Eight years later and based on a study of three species, van der Hammen (1965) suggested that the number of notogastral fissures, the position of the vestigial seta f_1, the number of adanal setae and the chaetotactic pattern of the legs were features which could be used in a future subdivision of the genus, and placed *P. laevigatus* and *P. nitens* (*ip* and *ips* present; f_1 ventral to h_1; ad_{1-2} absent; femur I with four setae; genu IV with a single seta) in a separate group from *P. anonymum* (*ip* and *ips* absent; f_1 dorsal to h_1; ad_{1-2} present; femur I with three setae; genu IV without any setae). Although the number of adanal setae has been found to be uncorrelated with other morphological features, the present study supports van der Hammen's proposed division of the genus on the remaining characters. Of the eight British species having the combination 'femur I-4, genu IV-1', only *murphyi* and *rectisetosus* have *all* the attributes of van der Hammen's '*laevigatus–nitens* group', since the other species (*affinis*, *clavatus*, *globus* and *juvenalis*) all lack the fissures *ip* and *ips*. In the case of species having the combination 'femur I-3, genu IV-0', only *P. anonymum* possesses all the characters of van der Hammen's second grouping.

Using numerical methods, Sheals (1969) examined the affinities of 19 *Phthiracarus* species from Europe, Israel, Labrador and Morocco, recognizing three species groups based on the following combinations of characters: femur I-4, genu IV-1, fissure *ips* present; femur I-4, genu IV-1, fissure *ips* absent; femur I-3, genu IV-0, fissure *ips* absent. It is noteworthy that *P. anonymum* which in the present study was found to be rather atypical, formed part of a reasonably compact cluster of five species in this grouping studied by Sheals (*P. anonymum* and four new species from France, Labrador, Sweden and Switzerland).

The evidence suggests therefore, that morphological differences, particularly in the leg chaetotaxy, could provide a useful basis for dividing this large genus into two species groups. In the present study all the British species (and all the type specimens examined) fell into either a 'complete' (*affinis*, *clavatus*, *globus*, *juvenalis*, *laevigatus*, *murphyi*, *nitens* and *rectisetosus*) or a 'reduced chaetotaxy group' (*anonymum*, *flexisetosus*, *membranifer*, *serrulatus* and *tardus*). In addition to features of the leg chaetotaxy, a number of other characters were also used to distinguish between the two groupings. With the exception of *P. affinis* (notogastral length 406 – 487 μm), the species in the 'complete chaetotaxy group' are all rather large (notogastral length 502 – 1065 μm). Moreover, in this grouping, the vestigial seta f_1 is generally ventral to seta h_1 while on the aspis the rostral setae are always located rather close together. The fissures *ip* and *ips* are present in some members of the 'complete group' (*laevigatus*, *murphyi*, *nitens* and *rectisetosus*) while they are absent in *affinis*, *clavatus*, *globus* and *juvenalis*. By contrast, species in the 'reduced chaetotaxy group' are all relatively small (notogastral length 314 – 507 μm), the fissures *ip* and *ips* are always absent, vestigial f_1 is dorsal or slightly ventral to seta h_1 and on the aspis the rostrals are often located relatively far apart.

Any formal subdivision of the genus will, however, have to be deferred until a new type species has been designated. Van der Hammen (1965) considered *P. contractilis* (type) as being close to his '*laevigatus–nitens* group' (and thus to the 'complete chaetotaxy group'), but the type material of *P. contractilis* must be presumed to be lost and Perty's original description is such as to make the specific identity of his species impossible. Moreover, on the evidence available from the present study, *P. anonymum* would not be a suitable typical specimen of the 'reduced chaetotaxy group'.

Acknowledgements

This paper is based substantially on part of a Ph.D. thesis (Parry, 1976) undertaken at the BMNH. The work was supervised jointly by Dr J. G. Sheals, Keeper of Zoology, BMNH, and by Dr J. A. Wallwork of the Zoology Department at Westfield College (University of London). Their valuable advice and encouragement are gratefully acknowledged. Thanks are also due to my colleague, Mr D. Macfarlane, for his comments on the manuscript.

Type material was kindly sent on loan by Dr J. Aoki, National University of Yokohama (NUY), Dr L. van der Hammen, Rijksmuseum van Natuurlijke Historie (RNH), Leiden and by Dr C. Pérez-Iñigo, Instituto Español de Entomologia (IEE), Madrid. Specimens from the Berlese and Willmann Collections were examined through the courtesy of Dr F. Pegazzano, Istituto Sperimentale per la Zoologie Agraria (ISZA), Florence, and Dr W. Hirschmann, Nürnberg respectively. Dr R. E. Crabill, National Museum of Natural History (USNM), Washington, arranged for the loan of type material described by Ewing and Woolley, and Dr H. W. Levi, Museum of Comparative Zoology (MCZ), Cambridge, Massachusetts, allowed me to borrow the type material of Bank's and Jacot's species. Dr J. Travé, Université Pierre et Marie Curie (UPMC), Banyuls-sur-Mer, kindly provided topotypic material of Grandjean's species and Dr S. L. Tuxen, University of Copenhagen Zoological Museum (UZM), sent type material of species described by Marie Hammer. I am grateful to Dr T. G. Wood, formerly of the Animal Ecology Research Group, Oxford, for material collected at Wytham Woods Estate, Berkshire.

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Appendix 1

Species described between 1763 and 1977 currently classified in *Phthiracarus*

Species	Date	Type habitat and locality	Type depository*
Hoploderma affine Hull†	1914	Moss in woods and *Sphagnum* on moors, West Allendale, Northumberland and Gibside, Durham, England	BMNH, London
Phthiracarus anonymum Grandjean†	1933	Rotting wood in cellar, Périgueux, Dordogne, France	UPMC, Banyuls-sur Mer [Topotype]
Phthiracarus anonymus amicus Jacot†	1938	Deciduous leaf mould, Connecticut Hill, New York, USA	MCZ, Cambridge, Mass.
Phthiracarus apiculatus Jacot	1939	Oak litter in old growth stand, Bent Creek Exp. Forest, North Carolina, USA	[Type series apparently lost]
Phthiracarus baloghi Feider & Suciu	1957	Oak leaves, Iaşi, Rumania	Unknown
Phthiracarus benoiti Balogh	1958	Angola	TM, Budapest
Hoploderma boreale Trägårdh†	1910	Rotting birch leaves, Sarek, Swedish Lapland	BMNH, London ['Cotype']
Phthiracarus boresetosum Jacot†	1930	Haircap moss in woodland, Cliff Island, Casco Bay, Maine, USA	MCZ, Cambridge, Mass.
Phthiracarus brevisetae Jacot†	1930	Decaying grass at foot of old haystack, East Village, Monroe, Connecticut, USA	MCZ, Cambridge, Mass.
Phthiracarus caudatus Balogh & Mahunka	1977	Moist soil in virgin forest, Estancia Esperanza, Guayaramerin, Bolivia	TM, Budapest
Phthiracarus clemens Aoki†	1963	Imperial Palace Gardens, Tokyo, Japan	NUY, Yokohama [badly broken]
Phthiracarus compressum Jacot†	1930	Upland swamp *Sphagnum*, East Village, Monroe, Connecticut, USA	MCZ, Cambridge, Mass.
Phthiracarus contractilis Perty‡	1841	Rotting wood, Munich, Augsberg and Passau, West Germany	[Type series apparently lost]
Phthiracarus crenophilus Willmann†	1951	Edge of marsh, Ebreichsdorf, Austria	Hirschmann Coll., Nürnberg

Species	Date	Type habitat and locality	Type depository*
Hoplophora crinita Koch	1841	Moss in woods, Regensburg area, West Germany	[Type series apparently lost]
Phthiracarus crispus Hammer†	1972	Rotting leaves and moss (altitude 600 m), Papeete, Tahiti	UZM, Copenhagen
Phthiracarus curtulus Berlese†	1923	Lake City, Florida, USA	ISZA, Florence
Phthiracarus danubianus Feider, Vasilu & Călugăr	1968	Moss and leaves, Cazanele Mici, Rumania	Unknown
Oribates dasypus Dugès‡	1834	Ardennes, France	[Type series apparently lost]
Phthiracarus dubinini Feider & Suciu	1958	Hornbeam litter, Constanţa, Rumania	Unknown
Phthiracarus feideri Balogh & Csiszár	1963	Litter and moss on bark in marsh forest, Río Negro, El Bolsón, Argentina	TM, Budapest
Hoplophora ferruginea Koch	1841	Moss on trees, Regensburg area, West Germany	[Type series apparently lost]
Phthiracarus globifer Hammer†	1962	Meadow near river, Copiapó, Chile	UZM, Copenhagen
Hoplophora globosa Koch	1841	Damp meadows, Regensburg area, West Germany	[Type series apparently lost]
Phthiracarus hamatus Hammer†	1973	Dry bark on deciduous tree, Tongatapu Island	UZM, Copenhagen
Phthiracarus insularis Balogh	1962	La Mandraka, Madagascar	TM, Budapest
Phthiracarus insularis Jacot	1935	Dead leaves, Teuanui, Tovii (altitude 2000 ft), Marquesas Islands	[Type series apparently lost]
Hoploderma italicum Oudemans‡ (=*Oribates dasypus* Dugès *sensu* Berlese)	1907	Tiarno, Italy	ISZA, Florence
Phthiracarus jacoti Feider & Suciu	1958	Spruce and fir needles Braşov, Rumania	Unknown
Phthiracarus japonicus Aoki†	1958	Raw humus under conifers, Matsumoto, Japan	NUY, Yokohama [badly broken]
Hoplophora laevigata Koch†	1841	Clubmosses and soil under hedges and bushes, Regensburg area, West Germany	RNH, Leiden [Neotype]
Phthiracarus lanatus Feider & Suciu	1957	Moss, Odorhei, Mureş-Magyar, Rumania	Unknown
Hoplophora lentula Koch	1841	Moss in woods, Regensburg area, West Germany	[Type series apparently lost]
Phthiracarus ligneus Willmann†	1932	Humus, moist *Juncus* and moss on the Dummersdorf bank, River Trave, West Germany	Hirschmann Coll., Nürnberg
Hoplophora longula Koch	1841	Moss in forests, Regensburg area, West Germany	[Type series apparently lost]
Hoplophora lucida Koch	1841	Marshy places in meadows, Regensburg area, West Germany	[Type series apparently lost]
Hoploderma lurida Ewing†	1909	Under bark, Urbana, Illinois, USA	USNM, Washington
Phthiracarus machadoi Balogh	1958	Angola	TM, Budapest
Phthiracarus minimarginatus Woolley†	1954	Moss and grass under aspen, Mount Meeker Camp Ground, Boulder, Colorado, USA	USNM, Washington
Phthiracarus montanus Pérez-Iñigo†	1969	Grassland soil and moist moss, Sierra de Guadarrama, Spain	IEE, Madrid
Phthiracarus montium Jacot	1937	Litter in short-leaf pine stand, Ashville, North Carolina, USA	[Type series apparently lost]

Species	Date	Type habitat and locality	Type depository*
Phthiracarus murphyi Harding†	1976	Beech litter, Lambridge Wood, Oxfordshire, England	BMNH, London
Phthiracarus nigerrimus Berlese†	1920	La Plata, Argentina	ISZA, Florence
Hoplophora nitens Nicolet†	1855	Litter in woods near Paris, France	RNH, Leiden [Neotype]
Phthiracarus olivaceus Jacot†	1928	Soft moist soil, East Village, Monroe, Connecticut, USA	MCZ, Cambridge, Mass.
Phthiracarus pallidus Feider & Suciu	1958	Beech litter, Iaşi, Rumania	Unknown
Phthiracarus parabotrichus Feider & Suciu	1957	Leaves, Iaşi and Constanţa, Rumania	Unknown
Phthiracarus pavidus minus Krivolutsky	1966	Blagoveschensk, USSR	Unknown
Phthiracarus pellucidus Ramsay	1966	Halophytic scrub and mat plants, Little Brother Island, Cook Strait, New Zealand	DSIR, Nelson & BMNH, London
Phthiracarus peristomaticus Willmann‡	1951	Number of habitats including leaves, turf and subsoil under buckthorn, guelder-rose and alder, near Vienna, Austria	[Type series apparently lost]
Acarus piger Scopoli‡	1763	Encrusting lichens, Carniola ('Karniolie'), Yugoslavia	[Type series apparently lost]
Phthiracarus ponticus Krivolutsky	1975	Unknown	Unknown
Phthiracarus prior Jacot	1933	Gainesville and East Palatka, Florida, USA	[Type series apparently lost]
Phthiracarus pudicus Berlese†	1923	Cape of Good Hope, South Africa	ISZA, Florence
Phthiracarus pygmaeus Balogh	1958	Angola	TM, Budapest
Phthiracarus restrictus Jacot	1937	Litter in rocky cove, Bent Creek Exp. Forest, North Carolina, USA	[Type series apparently lost]
Phthiracarus robertsi Sheals†	1965	Rhododendron litter, Milke Danra, Nepal	BMNH, London
Phthiracarus rotundus Berlese†	1923	Citta di Castello, Italy	ISZA, Florence
Phthiracarus roubali Berlese†	1923	'Boemia (Brady)', possibly Czechoslovakia	ISZA, Florence
Phthiracarus sarahae Jacot†	1930	Spruce needles, Cliff Island, Casco Bay, Maine, USA	MCZ, Cambridge, Mass.
Phthiracarus sellnicki Feider & Suciu	1957	Conifer needles, Braşov and Ploieşti, Rumania	Unknown
Phthiracarus serrula Balogh & Mahunka	1977	Gallery forest along River Mamore, Estancia Esperanza, Guayaramerin, Bolivia	TM, Budapest
Phthiracatus setanus Jacot	1939	Litter in laurel slick, Bent Creek, Exp. Forest, North Carolina, USA	[Type series apparently lost]
Hoplophora setosa Banks†	1895	Sea Cliff, New York, USA	MCZ, Cambridge, Mass.
Phthiracarus setosellum Jacot†	1928	Rotten wood and bark slabs, Glen Cove, Long Island, New York, USA	MCZ, Cambridge, Mass.
Phthiracarus setosellum bryobium Jacot*	1930	Upland swamp moss, East Village, Monroe, Connecticut, USA	MCZ, Cambridge, Mass
Phthiracarus sicilicoma Hammer†	1962	Meadowy vegetation under trees, Puerto Montt, Chile	UZM, Copenhagen
Hoplophora sphaerula Banks‡	1895	Sea Cliff, New York, USA	[Type series apparently lost]

Species	Date	Type habitat and locality	Type depository*
Hoplophora straminea Koch	1841	Moss on trees, Regensburg area, West Germany	[Type series apparently lost]
Phthiracarus subglobosus Berlese†	1923	Vallombrosa, Italy	ISZA, Florence
Phthiracarus tardus Forsslund†	1956	Humus under *Vaccinium* in coniferous forest, Degerfors, Västerbotten, Sweden	NR, Stockholm & BMNH, London [Paratype]
Hoplophora testudinea Koch	1841	Moss on trees, Regensburg area, West Germany	[Type series apparently lost]
Phthiracarus torosus Willmann	1939	Leaves, Levado do Inferno, Madeira	[Type series apparently lost]
Phthiracarus tubulus Hammer† (=*lapsus calami* for *Hoplophthiracarus tubulus*)	1972	*Cyperus* litter near coast, Tahiti	UZM, Copenhagen
Phthiracarus undatus Oudemans‡	1915	Paris area, France	[Type series apparently lost]

* With the following exceptions, DSIR (Department of Scientific and Industrial Research), Nelson, NR (Naturhistoriska Riksmuseet), Stockholm, and TM (Természettudományi Múzeum), Budapest, explanations of depository abbreviations are given with the Acknowledgements.

† Specimens examined during the course of the present study.

‡ Species regarded as *nomina dubia*.

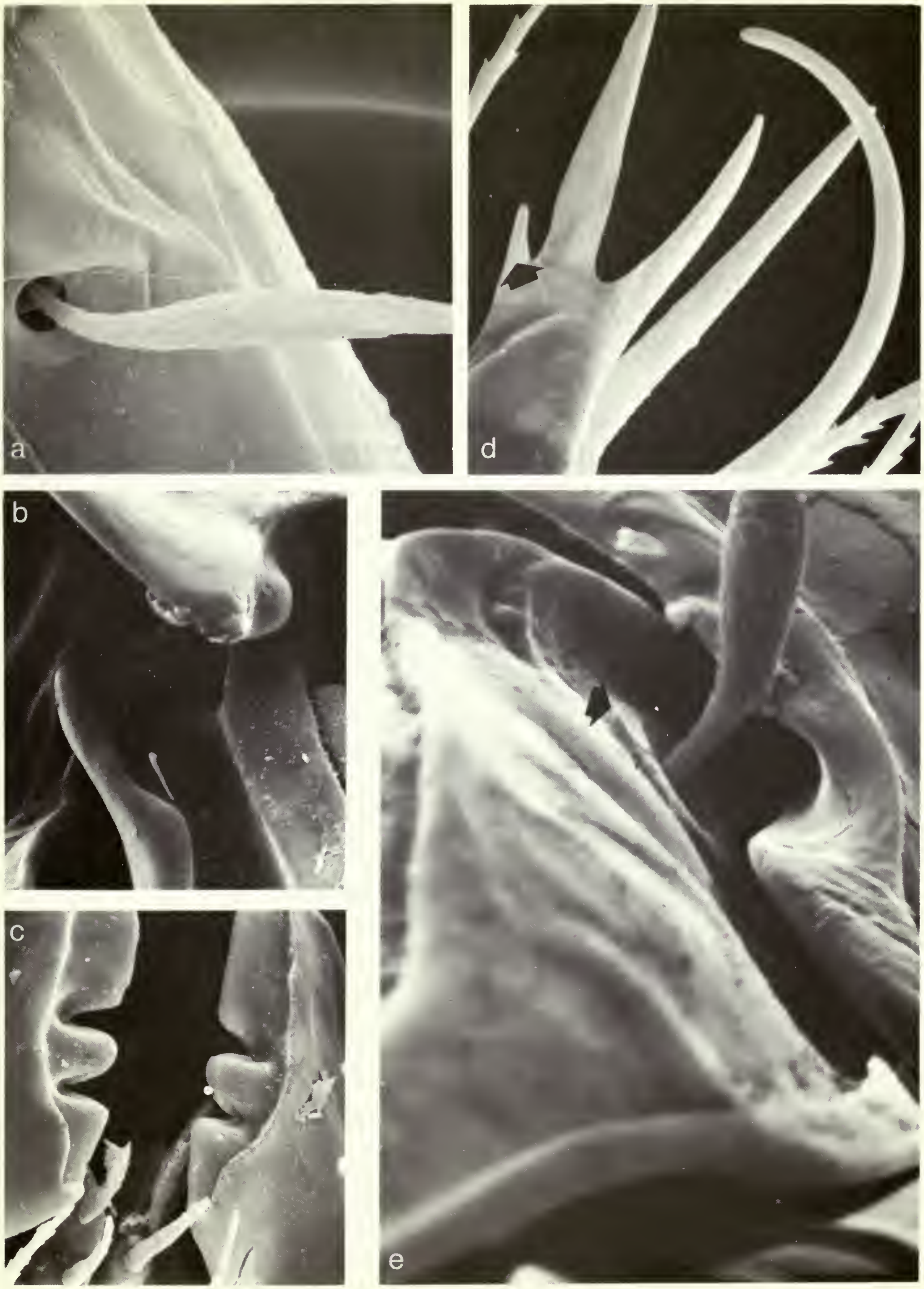

Plate 1 *Phthiracarus affinis*: idiosomal and gnathosomal features. (a) Sensillus and bothridial scale, ×2400. (b) Aggenital seta in furrow of genital plate, anterior aspect, ×1300. (c) Adoral setae and rutella, ventral aspect, ×1300. (d) Terminal segment of pedipalp showing reduced subultimal seta, ×1450. (e) Sensillar notch and thickened bothridial aperture, ×1500.

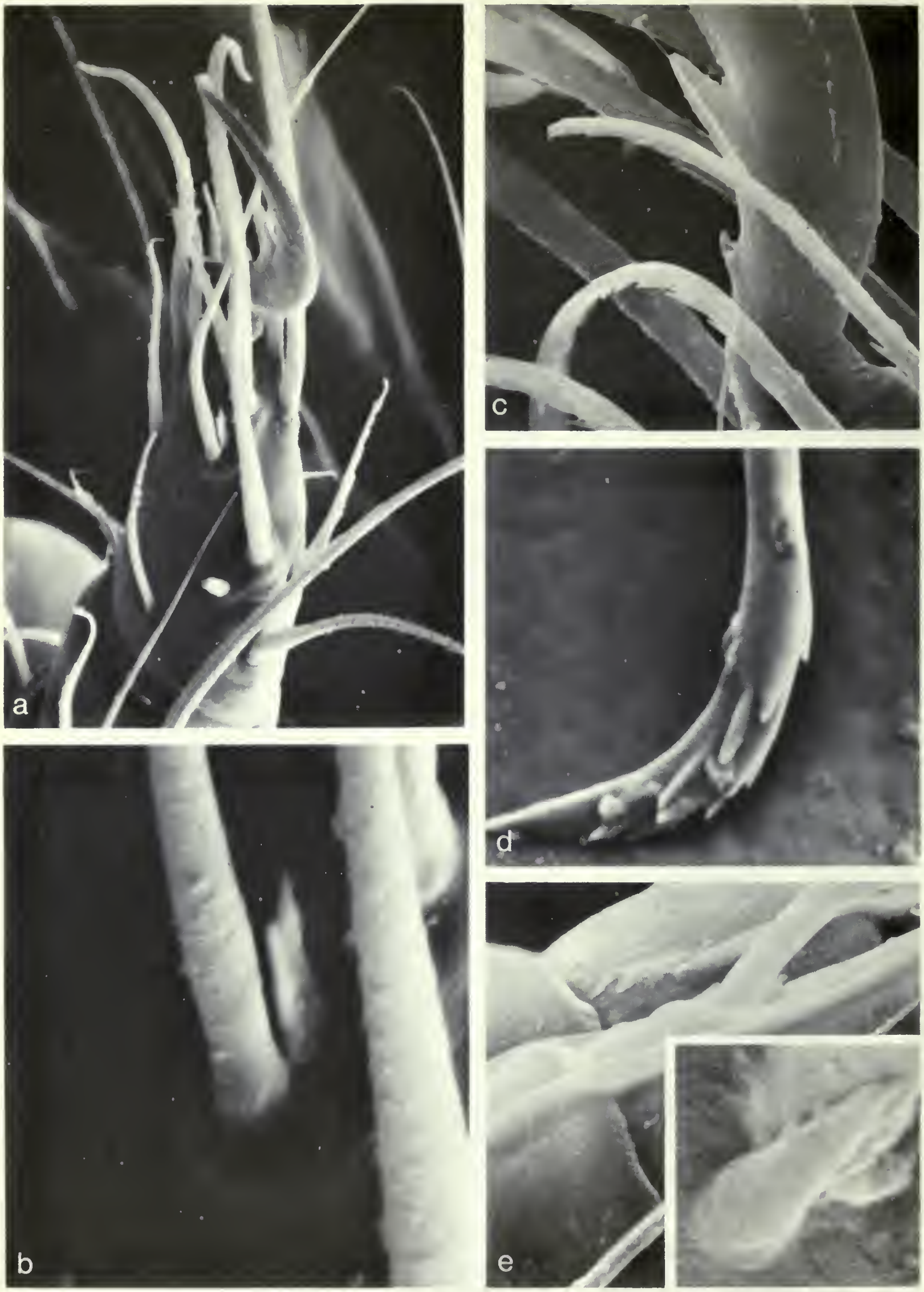

Plate 2 *Phthiracarus affinis*: legs. (a) Tarsus I, anterolateral aspect, ×1100. (b) Distal solenidion and associated seta on tarsus I, posterolateral aspect, ×5100. (c) Proximal region of tarsal claw, anterolateral aspect, ×1700. (d) Dorsal seta on femur I, ×4800. (e) Solenidion and associated seta on tibia II, anterolateral aspect, ×2400; dorsal aspect, ×15 000 (shown in inset).

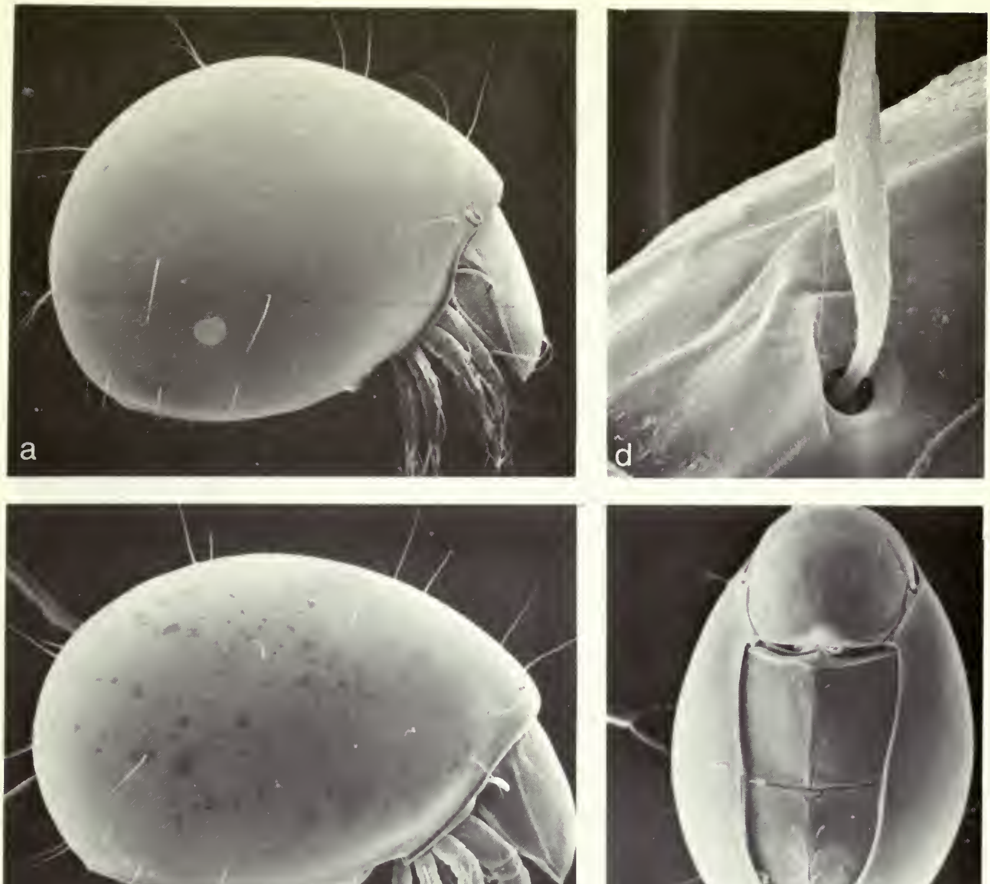

Plate 3 *Phthiracarus* spp.: (a) *P. affinis*, lateral aspect, ×60; (b) *P. anonymum*, lateral aspect, ×130; (c) *P. clavatus*, lateral aspect, ×100; (d) sensillus of *P. affinis*, ×1500; (e) *P. anonymum*, ventral aspect, ×120; (f) sensillus of *P. clavatus*, ×1900.

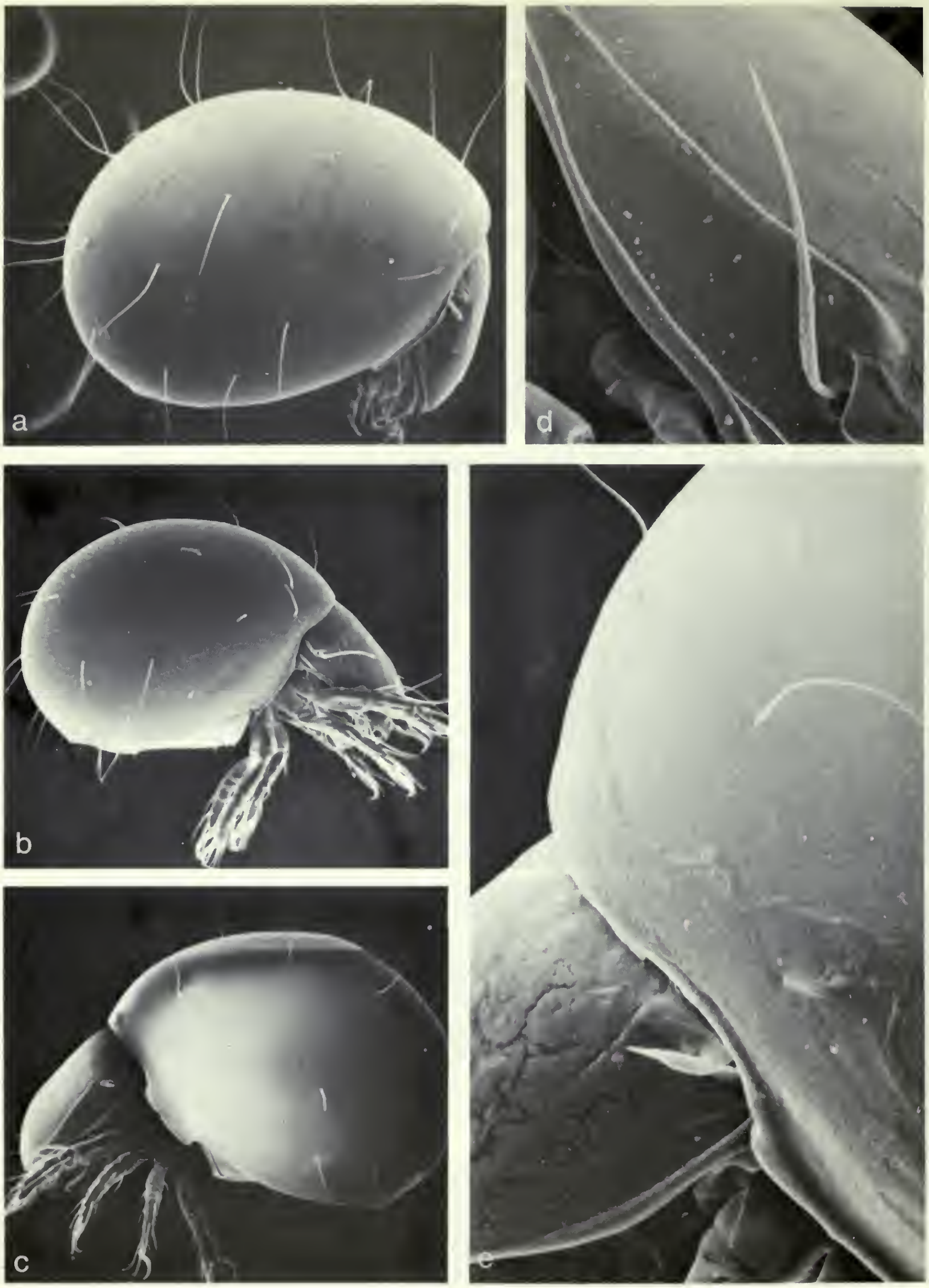

Plate 4 *Phthiracarus* spp.: (a) *P. globus*, ×150; (b) *P. juvenalis*, ×80; (c) *P. murphyi*, ×60; (d) sensillus of *P. juvenalis*, ×600; (e) *P. laevigatus*, ×350. All mites shown in lateral aspect.

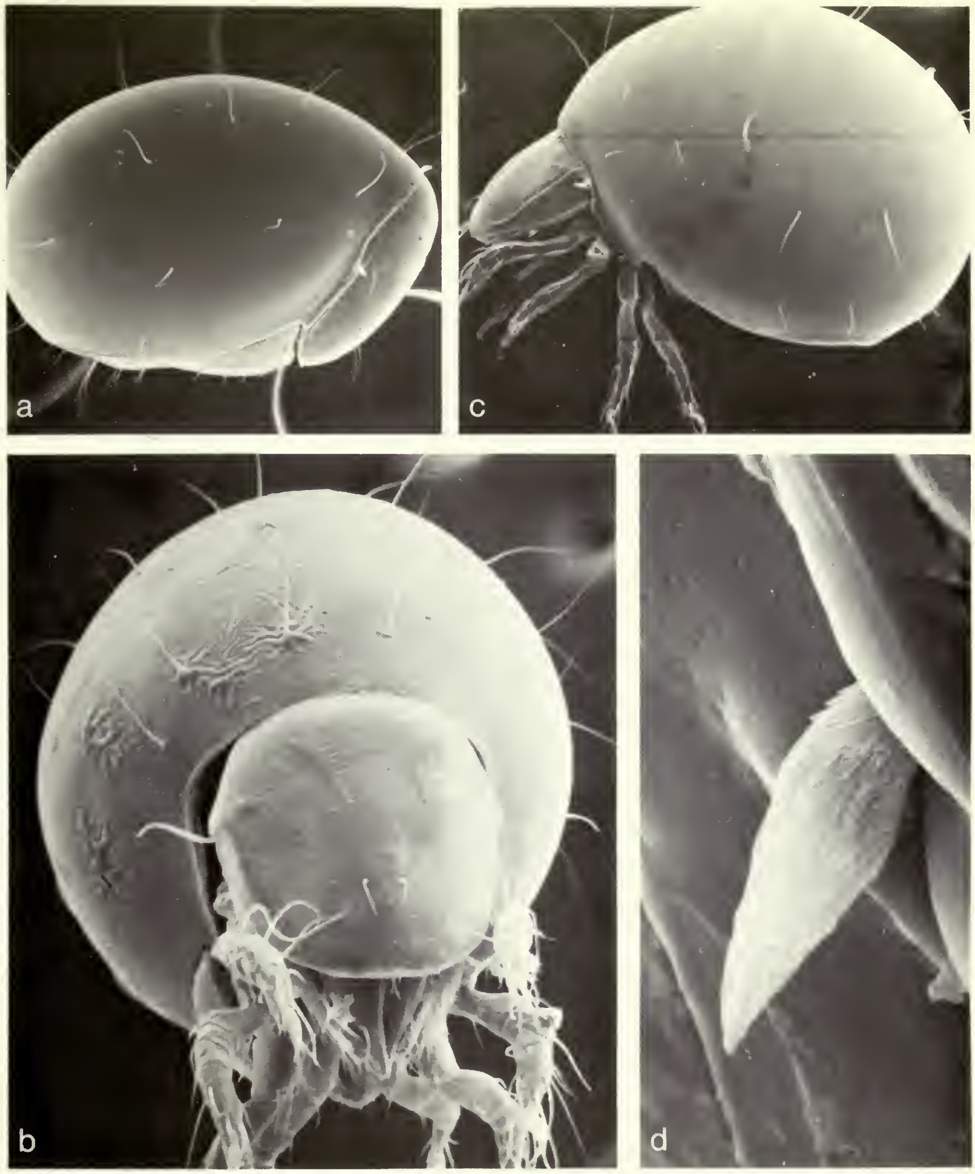

Plate 5 *Phthiracarus* spp.: (a) *P. tardus*, lateral aspect, ×100; (b) *P. serrulatus*, anterior aspect, ×200; (c) *P. rectisetosus*, lateral aspect, ×60; (d) sensillus of *P. tardus*, ×2600.

Manuscript accepted for publication 3 May 1978

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